THE TERRESTRIAL HABITAT SELECTION AND UTILISATION BY THE COMMON TOAD (Bufo bufo L.) IN AGRICULTURAL LANDSCAPES

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ABSTRACT

An established common toad population, within a functional arable estate, was studied from 1991-1994 in an attempt to explain the variation in the adult population through habitat use. Data obtained were from trapping studies completed over the breeding season and during metamorph emergence. Drift fences and habitat enclosures were placed in contrasting habitats (woodland, rough pasture, hedge and arable fields) to provide an assessment of the relative merits of each. The habitat selection and utilisation patterns for individual toads were obtained through radio-tracking. Animals were released into a specially constructed enclosure and their movements were monitored by an automated radio-tracking system. Further radio-tracking studies were conducted at the arable estate.

Trapping studies showed consistently higher adult densities in the woodland blocks (200-600 toads/ha) than adjacent arable fields (20-50 toads/ha). Adult density was higher in deciduous woodland (430 ± (S.E.) 110 toads/ha) than in coniferous woodland (150 ± (S.E.) 54 toads/ha). Adult density within a typical fragmented agricultural landscape was highest in areas of woodland within 100m from the breeding pond. Within a fragmented landscape density was negatively correlated with increasing distance from the breeding site, although studies in a more homogenous landscape suggested that density remained consistent. Fragmentation of woodland with inferior habitat (eg. arable fields) reduces adult density in woodlands separated from the breeding site. Trapping results indicated a high fidelity to former ranges regardless of quality.

A clear sex differential was shown in the selection of over-wintering location, with a higher sex ratio observed in traps within 100m from the pond than more distal traps. Females are believed to disperse more widely during their juvenile years and over winter at locations further from the pond than males. Males select over wintering locations close to the pond to improve their opportunity for pairing.

Female condition, based on a ratio between length and mass was not statistically different between contrasting habitats, suggesting a minimum condition required for breeding. However, clear discrepancies occurred in the age at first breeding, with females generating from woodland habitats reaching maturity earlier than those from arable habitats. There were significant differences in male condition between habitats, with animals migrating from the east of the breeding pond in better condition than those from the west. There was no significant difference in the lengths of either males or females generating from contrasting habitats. Males may attempt to breed regardless of body condition, however a minimum size is required prior to first breeding. Small males migrated to the pond later in the breeding season when pairing opportunities were therefore higher.

Adult male survival in the wooded habitats was almost twice that estimated in the arable areas. Adult survival in the woodland, pasture and arable habitats remained fairly consistent throughout the current study. Female survival was lower than male survival, reflecting the increased mortality over the breeding season, and the addition resources required for egg production. Annual growth rate was highest during the first six-months post-metamorphosis and declined during the life-time of the individual. Juvenile growth rates were higher in woodland areas with a dense ground cover. Adult growth rates were highest in woodland areas.

Breeding success was variable with total emergence ranging from over 200,000 to less than 2,000. The cause of the variation was not clear, although appeared unrelated to the number of adults breeding. Dispersion into the terrestrial habitat after emergence is considered to be random, based upon the location of the individual immediately prior to metamorphosis. Terrestrial ranges are therefore selected by random and maintained throughout the life-time of the individual. The adult population size declined over the study and this appeared to be the result of poor breeding success in previous years. Life-table analysis showed that breeding success and metamorph-juvenile survival during the first six months was the most powerful force in shaping adult population size.

Toads were highly sedentary during radio-tracking over the summer, with some females remaining within their refugium over periods of 14 days. Activity by toads in a woodland habitat was more extensive and frequent than for toads released into arable fields. Males released into the enclosure showed preference to the woodland habitat over the other available habitats in selecting their ranges. Female toads selected the rough pasture as their preferred habitat, although unlike the males, these differences were not statistically significant.

The agricultural landscape may be graded in favour of woodland followed by pasture and arable in terms of the adult density, adult survival, growth and rate of maturity. Within the broad category of woodland, deciduous woodland was graded higher than coniferous woodland and this differential is based upon the shrub and ground layer available within deciduous woodland that is considered to be beneficial to the toad, especially at the juvenile stage. However, the strong fidelity to habitats exhibited by the toads suggests that fidelity may be more important in determining habitat selection than habitat quality *per se*.

The terrestrial habitat selection and utilisation by the common toad (*Bufo bufo* L.) in agricultural landscapes.

Abstract

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Chapter One: The terrestrial ecology of the common toad

1.1 Introduction

Research on amphibian ecology has emphasised the importance of the breeding site in explaining amphibian presence or absence in geographical locations (eg Bell 1970, Cooke 1972, Cooke and Fraser 1976, Fraser 1983). However, amphibians require both aquatic and terrestrial habitats during their life histories. The common toad (*Bufo bufo*) spends the least proportion of its annual time budget in water of all U.K. amphibians; thus the quality of terrestrial landscape has a critical influence on species survival. Despite this, there has been limited study on the terrestrial element of amphibian ecology (the major exceptions to this being Strijbosch 1980, Beebee 1981, Swan 1986, Swan and Oldham 1993).

The aim of the current study was to identify the factors that govern toad population dynamics in terms of the use of available habitats. Through this it may be possible to explain observed amphibian decline in agricultural landscapes and recommend steps to reverse such declines (Hilton-Brown and Oldham 1991, Swan and Oldham 1993).

1.2 Amphibian status

Declines in the status of all amphibia were reported over most of the British Isles during 1940-1950 (Taylor 1963), with the speed of decline accelerating in the 1960s (Cooke 1972), but slowing during the 1980s (Hilton-Brown and Oldham 1991). The crested newt has suffered the greatest decline of all the common species receiving full protection under the Wildlife and Countryside Act (1981) and listed under Appendix IV under the European 'Habitats' Directive (Juniper 1994). Over the past 20 years the common frog has benefited from the increase in garden ponds (Beebee 1979, Latham, Bowen and Jeffcote 1994) and has increased its status in urban areas, despite serious declines in the rural landscape (Cooke and Scorgie 1983, Hilton-Brown and Oldham 1991). Although, toad status has not declined as much as the crested newt, its distribution across Britain is patchy. This patchy distribution could be a reflection of its exacting aquatic and terrestrial habitat requirements (Swan and Oldham 1993), since it is climatically adapted to colonise the whole of Britain.

Swan and Oldham (1993) link the decline in the status of amphibians in Britain to two main factors; changes in pond status and destruction of terrestrial habitat. The number of ponds in England and Wales was probably highest during the enclosure period (18th century) with approximately 800,000 present (Rackham 1986). Pond number may well have been artificially during this period, with field encloses require pond creation for cattle watering. Over the last 100 years numbers have fallen by as much as 68% (Probert 1989, citing Rackham 1986), with Oldham and Swan (1995) reporting a median loss equivalent to 6.5 ponds every ten years per 10km^2 estimated from 44 surveys carried out in 25 counties since 1764. The trend has accelerated over the period, with 0.5% of ponds lost per annum during the last 100 years, 1% during the last 50 years and 2% during the last 25 years.

Three main factors that are probably responsible for pond decline are changes in farming practice; urban encroachment and natural succession. Expansion of the agricultural system since the Second World War has resulted in intensification of farming practice. Changes in the availability grants and subsidies for farmers have encouraged drainage of fields previously unsuitable for agriculture, and piped water supplies for grazing cattle have both led to the loss of field ponds. In Nottinghamshire, 90% of agricultural ponds have disappeared over the last 50 years due to changes in land use (Probert 1989). Stupart (1986) attributed 50% of pond loss in the parish of Scraptoft, Leicestershire to urban expansion. Similarly, in Hampshire, a survey of rural villages indicated a loss of 14% of ponds due to housing developments (Probert 1989). Martin (1987) reported similar decline in the number of ponds in another Leicestershire parish, but attributed 68% of pond loss to natural hydroseral succession. This could be a result of lack of management following the redundancy of ponds for cattle watering (Probert 1989) or an increase in the speed of hydroseral succession caused by agricultural fertilisers.

The common toad is known to prefer established water bodies, usually associated with fish (Swan and Oldham 1993), and research in the U.K. has shown it to be slow to colonise new ponds, even where a vibrant source population is close by (Beebee 1986, Latham 1995) although it is believed to one of the first colonisers of new water ponds in Central Europe (Sinsch pers. comm.). Decline in pond status has a direct

impact on the number of potential breeding sites, but also the chances of colonisation of new ponds by dispersal from neighbouring sites. The larger fish ponds, favoured by the toad, are less likely to be lost through hydroseral succession, poor maintenance or changes in field drainage than the smaller ponds favoured by the crested newt. Where ponds contain fish, anglers may also help to maintain the breeding site. The loss, however, of 'stepping stone' ponds between toad colonies may reduce opportunities for colonisation and this might explain the toad's patchy status, especially given its apparently poor dispersal abilities.

Changes in the terrestrial habitat are typified by the substantial increase in the arable to pasture ratio (Chew 1953, Jones 1971) e.g. a change from 0.09 in 1934 to 0.61 in 1978 in the parish of Scraptoft, Leicestershire (Stupart 1986). This reflects an overall shift to arable land, estimated to be as much as 35% since 1945. The loss of the patchwork of mixed habitat has developed a landscape considered to be hostile to amphibians (Swan 1986). The expansion of the road network, in particular the construction of motorways has also had an impact on the terrestrial habitat, both through direct habitat loss and isolation of terrestrial habitats from breeding sites. Reh and Seitz (1990) have demonstrated that a busy road may be an effective barrier to dispersal for the common frog (*Rana temporaria*). Indeed the direct impact of road deaths may have less overall effect on the dynamics of an amphibian population than the indirect effects, for example, reducing the opportunities for colonisation of new sites.

Similar declines in amphibians to those in Britain have been reported in other parts of Europe (Beebee 1996) and are believed to be part of a global decline in amphibians (Wake 1991). Declines in Europe have been explained by loss of breeding sites, in the case of the crested newt (Oldham 1994), increase in disease, possibly the common frog in the U.K. (Cunningham *et. al.* 1993), destruction of habitats (Griffiths and Beebee 1992) or a combination of all. In other parts of the World, declines in areas of prime natural habitat are more perplexing; the golden toad (*Bufo periglenes*) and the harlequin frog (*Atelopus varius*) in the Monteverde Cloud Forest Reserve, Costa Rica (Pounds and Crump 1994) have both declined over the last decade without any obvious change in habitat. Where habitat destruction is not to blame, declines

have been attributed to climatic change, acidification or aquatic pollution (see reviews by Blaustein and Wake 1990, Blaustein 1994, Blaustein, Wake and Sousa 1994, Pechmann and Wilbur 1994).

Whilst the importance of these apparent declines should not be played down, it is equally important to distinguish between decline and natural fluctuation. Pechmann *et al.* (1991) monitored populations of three salamander and one frog species over the period 1979-1990 observing fluctuation in population size and recruitment of juveniles for all four species. Their data could not support a hypothesis of amphibian decline or show any overall trend in the breeding population size for any of the four species. Downward trends were often followed by recovery and species did not follow the same trends at the same time. Fluctuations have also been reported in population numbers for the smooth and palmate newt (Griffiths pers. comm.) and for the great crested newt (Cooke 1995). Fluctuations may thus be a natural part of the population cycle for amphibians. Nevertheless, there are long-term studies that do illustrate species decline. Semb-Johansson (1992) monitored a population of the common toad for 25 years witnessing a 90% decline in population size, attributed to acidification of the breeding ponds, acting through poor tadpole recruitment. Berger (1987) reported decline in 12 species of amphibians over 1965-1985 in areas of intensive agriculture in Central Poland, that he attributed to pollution of the breeding ponds by nitrogenous fertiliser. Ammonium nitrate and other common agricultural fertilisers have been shown to be toxic to the adult common frog, that may be partly responsible for the decline and failure of the frog to re-establish itself in rural areas (Oldham *et al.* 1993, Watt and Oldham 1995, Hecnar 1995).

1.3 Amphibian distribution and presence

Studies on the terrestrial requirements of amphibians have concentrated on establishing the habitat characteristics that explain presence or absence. This has been conducted at the individual population level, studying the density, selection and use of terrestrial habitats by amphibians at a breeding site (e.g. Karg and Mazur 1969, Roberts and Lewin 1979, Loman 1984, Oldham and Swan 1991, Denton and Beebee 1993a, Pasanen *et al.* 1993), by attempts to identify habitat features associated with simple presence or absence, or through form of multi-variate analysis (e.g. Beebee

1985, Laan and Verboom 1990, Pavignano, Giacoma and Castellano 1990, Mann, Dorn and Brandl 1991, Swan and Oldham 1993).

A higher density of toads is recorded in scrub and woodland habitats than in arable and pasture (Roberts and Lewin 1979, Oldham and Swan 1991, Swan 1986, Swan and Oldham 1993, Oldham, Swan and Gibbons 1996), although it is known that the toads will use open arable fields (Oldham and Swan 1992) and a variety of other habitats (Beebee 1981, Swan and Oldham 1993). Heusser (1968) reported a strong preference for woodlands by the toad over the intervening grassland habitat. In contrast, Strijbosch (1980) found the toad was more common in open habitats, pasture, meadows and agricultural areas. A review of available literature provides the density estimates for the range of habitats and species given Table 1.1, although comparison between the densities should be completed with some care considering the differences in sampling conditions.

Considering the wider distribution of the common toad, Beebee (1985) indicated a higher occupation of ponds located within greensands, heathlands and those containing fish by the common toad. Pavignano, Giacoma and Castellano (1990), however, working in north-west Italy could find no clear association explaining presence or absence of the common toad for their habitat characteristics (*extent of aquatic plant cover, age of pond, terrestrial habitats occurring near the pond, degree of human interference, pond surface area, maximum depth and water chemistry*). These largely aquatic characteristics provided the lowest percentage for success (<62%) in the discriminant classification used to predict the occurrence of the common toad out of their six target species. They concluded that the toad may colonise very heterogeneous habitats. Swan and Oldham (1993) used discriminant analysis to predict habitat requirements (both terrestrial and aquatic) for each of the five common amphibians in Britain. In homogeneous landscapes, eg. improved grassland and arable, the proximity of woodland to the breeding site provided a better prediction of toad presence than did the aquatic features (i.e. presence of fish, pond depth). In contrast, in heterogeneous habitats, eg. woodland or rough grassland, the important factors in explaining toad presence were aquatic. Studies on the occupation of ponds (Vos pers. comm.) within a predominantly agricultural landscape in The Netherlands,

TABLE 1.1: Adult densities (per hectare) for a range of anurans during their terrestrial phase. The range of density is given and, where provided, with standard deviation in parentheses and a short describtion of habitat type. 1: potato field; 2: mixed landscape domainated by farmland; 3: mixture of habitats including sedge, willow tall herb and poplar scrub; 4: Canadian spruce and upland mixed woodland.

Species	Habitat	Density (Ha^{-1})	Reference
Bufo bufo	Forest	100	Honjanina (1953)
	Orchard	70	
	Garden	140	
	Mixed	20	Oldham and Swan (1991)
	Mixed	340	Gittins (1980)
	Arable[1]	50	Karg and Mazur (1969)
Bufo hemiophrys	Tall-herb[3]	8.3-12	Roberts and Lewin (1979)
	High Forest[4]	1.6	
Bufo calamita	Heath	3 (+/- 0.2)	Denton and Beebee (1993a)
		48 (+/- 14.4)	
	Dune	8.6 (+/- 2.5)	
		6.3 (+/- 1.7)	
	Marsh	30.5 (+/- 27.6)	
		10.3 (+/- 2.5)	
Rana arvalis	Arable[1]	100	Karg and Mazur (1969)
	Forest	85	Garanin (1961)
Rana sylvatica	Tall-herb[3]	28.3-196	Roberts and Lewin (1979)
	High Forest[4]	10.8	
Rana temporaria	Conifer	64-80	Pasanen *et al.* (1993)
		25-50	Inozemtsev (1969)
	Meadow	550-790	Loman (1976, 1981, 1984)
	Deciduous	125	Glowacinski & Witkowski
Pseudracis triseriata maculata	Tall-herb[3]	4.5-23	Roberts and Lewin (1979)
	High Forest[4]	0.7	

by the tree frog (*Hyla arborea*) showed that the most influential factors in predicting pond occupancy were pond density and the area of tall herb, grass and shrubs within 1km of the pond edge. Laan and Verboom (1990) showed that pond age was the best predictor of amphibian diversity using a series of variables including pond size, isolation variables (including distance from nearest pond, field and wood), habitat variables (both terrestrial and aquatic) and pond age. Woodland was regarded as an important feature in increasing the connectivity of a landscape; a high level of connectivity was considered an important factor influencing the ability of amphibians to colonisation new ponds.

In contrast to the previous authors, Mann, Dorn and Brandl (1991) concluded that the degree of fragmentation increased the probability that a species would repopulate a pond from an adjacent one. Consequently, the probability that a certain species will be present somewhere in the whole landscape system increases as the landscape becomes more fragmented. These authors, however, assumed that the fragmented landscape was made-up only of habitats favourable to amphibian movements and this neglects the impact of roads, wide rivers and urban areas, for example, known to be barriers to amphibian dispersal (Arntzen pers. comm.). Motorways and railways have a significant barrier effect, as determined by the degree of genetic difference, on frog populations within 3-4km whilst the presence of meadows permitted exchange up to 7km (Reh and Seitz 1990). In addition, Mann, Dorn and Brandl (1991) assumed that the density of ponds remaining within the landscape remains at a level required by amphibians in maintain their presence in the region, for example Oldham and Swan (1993) have shown that a minimum density of 0.7 ponds/km^2 is required to maintain the presence of the great crested newt in Britain.

The above studies have attempted to explain amphibian presence on a geographical scale, either by evaluating habitat use at the population level or through describing habitat associations. Studies have concentrated on a single geographical location or population and have attempted to evaluate terrestrial habitat by estimating the observed density of individuals occurring in habitat types. The current study has attempted to estimate the adult density in a range of habitats, ranking them for their suitability for the common toad.

Despite published studies on the impact of climatic variation (Reading and Clarke 1995) on adult stomatic condition, I am aware of no published study on the role of the habitat on growth, survival, fecundity and stomatic condition in the common toad during the terrestrial phase. Data of these kind are important in prescribing management objectives for amphibians. In the current study the habitat preferences of an established toad population are investigated both at a macro-scale by estimating the density of toads in a range of habitats and at a micro-scale by studying utilisation within contrasting habitat types. The trapping studies in the current study during each breeding season aimed to provide the necessary data to allow comparison of a range of habitats using a series of ecological parameters (eg stomatic condition, survival, growth, density, age at first breeding, etc.).

1.4 The annual time budget of the common toad

Study of the time-budget of the toad allows assessment of the habitat requirements of the species throughout the year. The annual time budget of the common toad is characterised by three main periods (Sinsch 1988, Oldham and Swan 1991); breeding (Mar-April), late spring and summer movements (May-October) and hibernation (November-February), although these may be further classified into distinct sub-divisions.

1.4.1 Breeding migration

Common toads are explosive breeders (Wells 1977), with the adult population migrating *en masse* to the breeding site; the actual spawning period is normally limited to a week or two. Pre-breeding movements occur mainly during the evening and the stimulus is believed to be an increase in the dusk air temperatures, where night temperatures are consistently over 3-4°C (Heusser 1969, Wisniewski, Paull and Slater 1981, Griffiths, Harrison and Gittins 1986). There is believed to be limited toad migration below this threshold (Slater, Gittins and Harrison 1985). If temperatures fall once the breeding migration has started, the pattern of movement can be interrupted (Gittins, Parker and Slater 1980, Fraser 1983). Variation in spring temperatures is responsible for changes in the characteristics of the breeding migration because a cold early spring may delay the start of the migration and a warm early spring might encourage an early start to breeding. Highly variable temperatures may cause the

breeding migration to be disjointed.

The duration of the breeding period from the start of pre-breeding migration to final spawning is limited to only 25-46 days (Slater, Gittins and Harrison 1985). The number of days on which movement takes place, based upon a capture of at least 1% of the estimated adult population (Gittins 1983a), normally occupies only 10 to 11 days, given consistent climatic conditions (Slater, Gittins and Harrison 1985). Males arrive at the pond first and individuals may remain at the breeding site throughout the season (Gittins, Parker and Slater 1980, Gittins 1983a, Gittins 1983b), although there is also evidence of movement to and from the breeding site by males during the breeding season (Oldham pers. comm.). Females arrive at the breeding site after the main movement of the males and leave as soon as they have spawned (Sinsch 1988).

1.4.2 Late-spring and summer movements

Once the animals have left the water, after breeding, a period of inactivity is sometimes observed (Oldham and Swan 1991) with animals possibly located close to the pond edge. With warmer evening temperatures during late spring, animals are believed to move from their post-breeding retreats to occupy areas that will form their summer range.

Studies describing amphibian habitats in the previous section (2.2 and Table 2.1) suggest that there are higher densities of toads in woodland habitats. These offer a high invertebrate biomass for food (Cornish 1993) and plenty of dead wood and ground debris for cover (Latham, Bruce and Oldham 1994). These studies suggest that the utilisation of available habitats by the toad may be based on its requirement for food, cover and safety from predation. Selection of the initial home range must theoretically be based on ensuring the best available habitat for food and shelter. Fretwell (1972) suggests a theory of habitat selection where each available habitat is assumed to be suitable for the target species. In this example, suitability is affected by food supply, shelter and predation risk with changes in density of animals in each habitat influencing competition. As a landscape is filled, so the best habitat (that most *suitable* for the species) is used first. Density in best habitat rises to the point where a lower quality habitat becomes viable to occupy, given increases in competition for

resources, and this continues until all viable habitats are occupied.

Food availability has not been considered in the current study. The nature of habitat type has been studied through classification of each available habitat. The extent of use of refugia during the summer is not known and the availability of suitable hiding places may form the basis of selection of a habitat. The common toad uses vacant small mammal holes, log piles, areas of dense vegetation and leaf litter as refugia (Denton and Beebee 1992, Denton and Beebee 1993b). Refuge sites may play an important part in preventing predation or desiccation (Stewart and Pough 1983). During the current study adult toads were radio-tracked during their summer terrestrial period. This permitted identification and characterisation of the different forms of refugia in the study habitats and their use throughout the summer terrestrial phase.

Fretwell's theory suggests the occupation of patches through sequential filling of habitats of declining quality. Where landscapes may be saturated with a species, all viable habitats have equal suitability, but different densities. When the density of species within a landscape is low, only the best habitats are occupied. Fluctuations in the size of the resident population, and therefore the density, would thus lead to changes in the use of the viable habitats. This model assumes a level of habitat accessibility, which may not exist in the toad. Toads are far more restricted than birds and even small mammals in locomotion and therefore more restricted in the choice of habitats available to them around a breeding site. There have been no published studies for the common toad that have considered the use of habitats regarding suitability, or have considered the forces behind the initial selection of these home range areas. The development of an understanding of these concepts was a priority in the current study. In the current study, summer adult density has been used to predict habitat suitability, with individual habitats described by their vegetation structure and their distance from the breeding site.

1.4.3 Activity during the summer

Activity by anurans during summer is limited (Breckenridge and Tester 1961, Dole 1965, Mathias 1971, Denton and Beebee 1992, Swan and Oldham 1992), with studies indicating that animals may remain unmoved in their refugia for several days.

Movement is almost exclusively restricted to the evenings (Mathias 1971, Denton and Beebee 1992, Oldham and Swan 1992), although occasional day time movements may occur. Frequency of foraging excursions may be limited. Slater (1992) suggested that only 11-20 excursions per summer were required to accumulate sufficient food reserves for the over-winter period for the common toad. Any movements that do occur appear limited to only short foraging excursions. Breckenridge and Tester (1961) found daily movements of the Manitoba toad (*Bufo hemiophrys*) limited to less than 40m (using radio-active tags, see Chapter 4, section 4.2.2), similarly Dole (1965) found the movement of leopard frogs was often limited to only 5 to 10m between daily locations (using a trailing device, see Chapter 4, section 4.2.3). Oldham and Swan (1992) reported a that common toad, located on a daily basis using radio-tracking, remained stationary for long periods despite a maximum distance of 108m.

As in breeding migration, the climatic stimulus influencing summer activity appears to be air temperature, with little activity occurring below 10°C (Denton and Beebee 1992), although rainfall and humidity (*positive correlation*) and wind speed (*negative correlation*) have also been shown to have an influence on activity patterns (Heatwole 1961). The common toad is active during the day, but the majority of activity occurs during night. Grist (1994), in a review of Mathias' data (1971), acknowledged the influence of air temperatures and wind speed in controlling toad movements (for the natterjack as well as the common toad), but indicated a particular association between the higher numbers of toads caught and warmer underground temperatures (taken at 30cm below the ground surface) reported earlier the same day. He suggested that the underground temperature warmed the toads whilst in their burrows and this might encourage an evening foraging foray. Smits (1984) suggested the activity patterns of *Bufo boreas halophilus* may be controlled not only by minium temperatures, but also by maximum temperatures, and thus activity was restricted to a narrow band (10-25°C) throughout the year.

Differences in foraging patterns in contrasting habitats were studied in the current study to help explain any variation observed in the population. Toads were radio-tracked through contrasting habitats during the summer months. Air temperature and

humidity were recorded on site. Other weather variables were collected from the local newspaper.

The described pattern of activity shown by the species, *Bufo bufo, B. calamita* and *B. hemiophrys* (Breckenridge and Tester 1961, Mathias 1971, Denton and Beebee 1992, Swan and Oldham 1992) suggests a series of short movements based around a number of refugia that forms the foraging area or home range. The size of home range has been estimated by a number of researchers, Table 1.2. Denton and Beebee (1993) observed that the home-ranges occupied by natterjack toads in three separate study sites (lowland heath, sand dunes and saltmarsh) were larger when the density of individuals was high and there was, presumably, stronger competition for resources. It is clearly possible, however, that the physical characteristics of three separate study sites, consisting of lowland heath, sand dunes and saltmarsh or genetic characteristics of the population itself might control densities. Home range, may be a reflection of the suitability of a habitat, and be affected by density-dependent competition. There may also be sexual difference in the size of the home range within the population. It is has been established that females require an additional year to reach breeding maturity (Gittins, Steeds and Williams 1982, Gittins 1983b, Gittins 1983c, Gittins *et al.* 1985, Hemelaar 1986, Johnson 1992, Cooke and Oldham 1995), and therefore spend an additional year on land as a juvenile. Females also require additional food resources for egg production, growth and fat reserves for over-wintering, probably necessitating a larger home-range or more frequent foraging excursions.

Use of the same home-ranges in successive seasons has been observed by a number of researchers (Haapanen 1970, Haapanen 1974, Sinsch 1987a, Day 1889, Loman 1994) for several species of anuran. This tenacity extends to returning to established home ranges after translocation to a new location within the vicinity of the breeding pond (Oldham 1967, Dole 1974, Sinsch 1987a, Sinsch 1987b, Day 1989). However, Schlupp and Podloucky (1994) cite an instance of common toads resettling at a new site when a previous site became unavailable through dramatic change in habitat. Utilisation of the home ranges may alter during one season (Breckenridge and Tester 1961), with particular habitats favoured during different parts of the terrestrial season.

Table 1.2: Size of summer home range reported for several species of adult and juvenile anuran. Numbers in parentheses represent the sample size used to estimate the home range and standard deviation.

Species (n)	Life stage (n)	Area (m^2± SD)	Reference
Rana arvalis	adult (35)	534	Haapanen (1970)
	adult (78)	133	Loman (1994)
Rana temporaria	adult (23)	93	Haapanen (1970)
	adult (95)	330	Loman (1994)
Rana clamitans	adult (153)	380	Oldham (1967)
Rana pipiens	adult (28)	370	Dole (1965)
	juvenile (17)	280	
	adult (18)	90	
	adult (4)	80	
Rana pretiosa	juvenile (23)	534	Carpenter (1954)
Rana sylvatica	juvenile (298)	534	Bellis (1959)
Bufo americanus	adult (5)	21	Werner (1991)
Bufo boreas	juvenile (19)	627	Carpenter (1954)
Bufo bufo	adult (23)	1901 (± 312)	Sinsch (1987)
	adult (29)	59	Haapanen (1974)
	adult (3)	508 (± 247)	Denton and Beebee (1993a)
Bufo calamita	adult (28)	691 (± 601)	
	adult (5)	920 ±-650)	
	adult (7)	2160 (+/- 1232)	
Bufo hemiophryus	adult (19)	2827	Breckenridge and Tester (1961)
Bufo terrestris	not stated (27)	627	Bellis (1959)
Gastrophryne	adult (52)	4040	Fitch (1958)
Acris crepitans	not stated (34)	4810	Pyburn (1958)
Pseudacris triseriata	adult (9)	490	Kramer (1974)
Ascaphus truei	adult (101)	71 (± 28)	Daugherty and Sheldon (1982)

Fretwell's theory suggests that home ranges would be selected on merit, and the degree of use of each habitat would be variable given the overall size of the population. In the current study an attempt was made to understand how the initial selection of habitats was made, and how these were used in subsequent years to determine whether selection was on the basis of habitat quality. Data have been collected on the home range size, adult density, stomatic condition, survival and growth of individuals using distinct habitats. The current study has concentrated on the single site approach, with comparison between the individual habitats used by a single population. This approach helps to remove the difficulties faced by Denton and Beebee (1993a) in determining the effects that may be caused through density-dependence and habitat variability and those that may be due to characteristic of the individual populations themselves.

1.4.4 Metamorph dispersion

Size at metamorphosis is considered to be a reflection of the resources available during larval development for anurans (Wilbur and Collins 1973, Wilbur 1976, Wilbur 1977, Collins 1979, Dash and Hota 1980, Wilbur 1980, Werner 1986). Size advantage gained due variation in egg size may be maintained during the larval development for one species of salamander (Pechmann 1995). In *Rana clamitans*, given a limited food resource, larger tadpoles could out-compete smaller individuals for the available food; the competitively inferior smaller tadpoles consuming the lower quality food resources, normally faeces (Steinwascher 1979). This competitive interaction has the additional impact of increasing the parasite burden of the inferior individuals, resulting in reduced growth and lower survival. The larger tadpoles therefore maintain their advantage over the smaller animals by monopolizing the food resources that provide greater benefits and results in faster growth.

Tadpole development rates in the common toad are relatively consistent within the larval population; therefore emergence from the pond is normally *en masse* and completed within three weeks (Oldham 1985, Oldham and Swan 1991). Emergence from the pond is based on the location of the tadpole during the period immediately before metamorphosis, possibly linked to food availability and temperature regime within the pond. Dispersion from the breeding site is characterised by a progression

into the surrounding habitats, the speed of which is related to the ease of movement (Paull, Wisniewski and Slater 1981, Oldham and Swan 1991). This movement continues until the onset of colder autumnal weather resulting in the over-wintering of juveniles (Oldham and Swan 1991). The chance emergence from the breeding pond dictates the initial direction of dispersion and therefore has a strong influence on the overwintering habitat in the first year. An attempt has been made to consider the implications of the point of emergence from the pond on the life-history of the toad. Studies have concentrated on a single population using data collected over the period 1991 - 1994 from Osbaston Hall, Leicestershire.

1.4.5 Over-wintering

Since amphibians are poikilotherms there is no true hibernation as observed in some mammals, for example the dormouse *Muscardinus arvellanarius* (Corbett and Harris 1996), rather a reduction in animal activity as environmental temperatures fall. A slight increase in activity is observed in late autumn (Sinsch 1988, Oldham and Swan 1991) that might indicate a movement towards over-wintering sites. Sites for over-wintering are little different from these summer refugia (Breckenridge and Tester 1961, Denton and Beebee 1993), although it is likely that animals will attempt to move deeper into the substrate (Oldham pers comm.). Oldham and Swan (1991) recorded an increase in the number of toads caught in pitfalls surrounding a breeding site, during late September through the first half of October. This could be attributed to a move of adults towards the pond in anticipation of spring. This move might involve only males (Sinsch 1988); who would gain a competitive advantage in over-wintering close to the pond edge. In the subsequent breeding season early arrival might increase the opportunity to intercept a female.

1.5 Population dynamics

1.5.1 Population characteristics

The common toad produces a large number of offspring per female with no parental care and low survival. Adult females annually produce around 2000 eggs each (Slater 1992), although this figure is influenced by animal size (Davis and Halliday 1977, Gittins, Kennedy and Williams 1984, Swan 1986). Gittins (1983) and Gittins, Kennedy and Williams (1984) suggest only c. 0.1% of the eggs laid each year will reach

adulthood. Mortality in anurans is highest during the larval stage when as much as 95% of the tadpole population may die before metamorphosis (cited in Beebee 1996). On land annual adult mortality rate has been estimated as 50-60% (Gittins 1983a), although other research suggests it is as high as 90% (Reading pers. comm.). Little information is available for the juvenile phase of the toad, although it is likely that juvenile mortality is higher than adult mortality, as is widely observed in other species. Research completed during the current study for each of the life-stages of the population at Osbaston has been used to construct a life-table for the common toad.

Data derived from studies during the breeding season have shown that adult common toad populations are biased towards males (Moore 1954, Frazer 1966, Collier 1970, Davies and Halliday 1979, Gittins 1983a); sex-ratios can vary between 2:1 to 10:1 (Griffiths and Raper 1995). This sex-ratio has been explained by the difference in age of first breeding between males and females, although may be biased by the predominance of males at the breeding site. The youngest age at which toads have been shown to breed for the first time is two years for the male and three years for the female, though more typically three and four respectively (Gittins *et al.* 1982). Ageing of breeding individuals using skeletochronology (Hemelaar and van Gelder 1980) has been used to provide information on the age distribution within the population (e.g. Gittins, Steeds and Williams 1982, Gittins 1983a, Gittins 1983b, Gittins *et al.* 1985, Johnson 1992, Cooke and Oldham 1995). The longer maturation of the females increases their exposure to predation and so the sex-ratio of a population can be used to judge the level of adult mortality, and indirectly habitat quality. Where a sex-ratio is closer to 1:1 it suggests that a higher proportion of females is progressing to adulthood than in the case of a higher sex-ratio.

Trapping data from each of the habitats within the current study have been used to assess suitability using density, sex-ratio, size and stomatic condition of animals, inter-year survival and age at first breeding.

Predation has not been studied in depth for the common toad and existing information is largely from anecdotal sources. It was not an objective of the current study to define the nature of predation, except to establish its role in population regulation and

determine any variation between habitats. Seasonal exploitation of amphibians has been observed by the otter during the breeding season in areas where species distributions coincide (Weber 1990), but it is unlikely that this is a major predator during the remainder of the year. Predation during the breeding season by rats and corvid species is also likely at breeding aggregations. Predation during the terrestrial phase by the grass snake (Brown 1991, Franklin pers. comm.) and again by rats (Reading pers. comm.) has been observed.

1.5.2 Population dynamics and density dependence

Adult toad populations show a relatively high level of stability under consistent conditions (Gittins 1983a, Oldham pers. comm.) suggesting an effective density-dependent control mechanism. Two factors may indicate the presence of density dependent population regulation; the overall numerical size of the population and/or the size of the individual animal.

Changes in size of the adult population between years have been attributed to variation in larval success in both the wood frog, *Rana sylvatica* (Berven 1990, Berven 1994) and the chorus frog, *Pseudacris triseriata* (Smith 1987). In the latter, a long larval period and small body size at metamorphosis delayed adult maturity. Size advantage at metamorphosis has been shown to be maintained until adulthood for other species including the common frog (Augert and Joly 1993), and until the first hibernation for common toad (Goater 1994). Cohen and Alford (1993) illustrate a density dependent effect on the growth patterns of *Bufo marinus* metamorphs; with metamorphs at higher densities growing more slowly than those at lower densities.

Studies on *Bufo americanus* (Brockleman 1969, Wilbur 1977), *Rana slyvatica*, *R. tigrina* (Dash and Hota 1980), *Hyla gratiosa* (Travis 1984), *Scaphiopus couchii* (Newman 1994) and *Ambystoma* spp. (Wilbur 1976, Petranka and Sih 1986, Petranka 1989), *and Notophthalumus viridescens dorsalis* (Harris 1987) show density-dependent controls during the larval stage illustrated by increased mortality, small size at metamorphosis and a prolonged larval stage. As density increases, fewer individuals are able to complete metamorphosis (Wilbur 1977) due to increasing competition for food resources, assumed to be limiting (Wilbur 1977a, 1980). Low food levels

decrease average larval growth and average size at metamorphosis and increase length of the larval period (Travis 1984). A slower growth rate due to food competition prolongs the larval stage resulting in increased mortality (Dash and Hota 1980). Newman (1994), however, suggests that variation in density and food levels can cause an adaptation resulting in earlier metamorphosis, if at a smaller size.

Gittins, Kennedy and Williams (1985) suggest that adult size and mortality are a reflection of feeding conditions on land during the juvenile phase and that poor terrestrial conditions are a major influence on adult population dynamics. Variation has been shown to occur in the sizes of toads within an age class (Gittins *et al.* 1982, Hemelaar 1983, 1986, Johnson 1992, Augert and Joly 1993, Cooke and Oldham 1995).

Oldham and Swan (1991) noted a uniform size in emerging metamorphs at a single site in the common toad, yet distinct size variation has also been shown in adult toads generating from different habitats (Oldham, Swan and Gibbons 1996). This indicates that the variation in adult size might be a reflection of experiences post metamorphosis. Denton and Beebee (1993a) observed a density-dependent relationship in the adult natterjack toad; where individuals grew at a slower rate under high-density and the animals were in a poorer condition, although the vegetation characteristics at the sites where the data were obtained varied considerably. Longevity was inversely related to density, and thus the longer living females may be better indicators of density-dependence.

Further evaluation of the density-dependence mechanisms is required for a better understanding of the dynamics of a typical common toad population. The current study has approached this by collecting data on the density, survival, growth and stomatic condition of animals derived from a series of contrasting habitats. Life-table analysis has been used to indicate when population regulations may occur. By comparison of a series of ecological variables, an attempt has been made to identify the processes influencing population regulation and to establish their role in population dynamics.

Chapter Two: Research Objectives

2.1 Background

The research completed during the current study formed part of the study of 'Spatial Dynamics of Amphibian in Agricultural Landscapes' by De Montfort University (as Leicester Polytechnic) and the University of Leicester under the Joint Agriculture and Environment Programme (JAEP). The broad research objectives for this study were three fold:

(a) *To study the dispersal abilities of amphibia;*

(b) *To evaluate the extent to which amphibians are able to utilise the habitats available in agricultural landscapes; and*

(c) *To predict, categorise and explain the suitability of habitat.*

Dispersal was studied through analysis of the degree of genetic differentiation among a number of toad populations. Analysis of habitat utilisation was approached by the construction of habitat specific enclosures (HSEs) in the terrestrial ranges of the target species and the development of an automated radio-tracking system used in association with a test-enclosure. Categorization of individual habitats was completed through the study of habitat characteristics including the availability of food and cover. The National Amphibian Survey provided detailed information on over 1,500 ponds over the whole of Britain (Swan and Oldham 1993). This permitted multi-variate analysis of species assemblages and habitat types to explain distribution through habitat association. The relative merits of different habitats in harbouring a food supply for toads was investigated by sampling the invertebrate fauna and comparing this to toad diet (Cornish 1993, Cornish *et al.* 1995). Cover within individual habitats was evaluated by vegetation surveys using the National Vegetation Classification system and by assessment of the structure of the individual habitats.

2.2 Objectives of the current study

Four elements of the life-history of the toad have been investigated for the current study; *population dynamics, habitat selection and utilisation, division of annual time-*

budget and *habitat quality*. These have been examined through the specific objectives described below.

2.2.1 Population dynamics

The factors influencing population dynamics (i.e. population size, individual length, mass and stomatic condition, sex-ratio, survival, growth) were studied through annual censuses of the population during the breeding season when individuals were collected and length, mass and somatic condition recorded.

Specific objective: To determine the inter-year variation (*if any*) in population size, individual size and somatic condition.

It was hypothesised that the adult toad population would show a high level of stability under constant environmental conditions. Therefore any variation could be attributed to changes directly attributable to the characteristics of the population.

Specific objective: To explain the inter-year variation (*if determined*) in population size, individual size and somatic condition observed at the study site.

The construction of a life-table for the common toad facilitated identification of the stages within the toad's life history of most importance. It was hypothesised that the most important life stage in determining adult population size would be the number of breeding females each year, since this would control the number of eggs laid each year (given high mortality during the larval stage). Breeding toad populations have sex-ratios biased towards males, and males can breed more than once during each breeding season so their importance is decreased in comparison to that of females, that puts a limit on the total number of potential offspring.

2.2.2 Habitat use

The current study attempted to explain habitat selection and use by the common toad in an agricultural landscape. The habitat use illustrated by a species is a reflection of the suitability of that habitat for that species (sensu Fretwell 1972). By determining the suitability of agricultural habitats for the common toad, management recommendations for species conservation can be provided. In turn, defining critical habitat required by

the target species for survival, may help to explain the observed changes in species distribution and status as a reflection of changes in habitat composition in Britain. The adult density was determined through the construction of habitat specific enclosures in variety of habitats during appropriate periods of the year and which were effective during the breeding season.

Specific objective: **To quantify the density of toads found in a variety of common agriculture habitats.**

Swan (1986) concluded that woodland habitats and scrub habitats were of greater benefit, and therefore higher quality to toads than arable fields and closely grazed or cut grasslands. It was hypothesised that habitat density would reflect this initial evaluation of habitat quality, with the woodland and scrub habitats showing higher densities than the grassland and cultivated habitats.

Specific objective: **To evaluate the effects of agricultural practice on habitat utilisation by the common toad.**

It was hypothesised that the higher availability of food sources and cover in the arable fields available in the latter part of the summer would increase the value of these areas for toads, and encourage greater utilisation of arable areas at the expense of the woodland and scrub areas.

Arable farmland is neither natural nor remains free from disturbance (harvesting ploughing, fertilizing) and species utilising this habitat are faced with periods of change and disruption. It was hypothesised that harvesting would result in emigration from the arable fields into the surrounding woodland and headlands and a reduction in the use of the arable fields as part of the adult's home range. Toads were radio-tracked by hand throughout the summer (May-September) within an arable landscape before and after harvesting.

Specific objective: **To establish how adult home-range is established.**

Exodus from the pond as a metamorph is thought to be random with the metamorphs emerging into the surrounding landscape in an ever increasing wave until a change

in the weather causes over-wintering (Oldham 1985). Selection of the over-wintering habitat is therefore by chance, governed by the random location of the pre-metamorphic animals in the natal pond. Tenacity to summer home range has been shown to be high in the common toad for both adults and pre-adults, with individuals returning to habitats used in previous seasons (Haapanen 1974). It was hypothesised that summer home ranges were selected on the basis of random emergence from the pond and maintained in subsequent year through familiarity. The fidelity of adults to former ranges could be identified by the study of catch data and by matching identification tags over the course of the current study.

2.2.3 Time budgets

Data on the activity and habitat selection of the toad provides information beneficial for the conservation management of landscapes for the benefit of the target species.

Specific objective: **To identify the changes in seasonal activity.**

Migrations during the spring are characterised by large scale movements, with the adult population converging *en masse* to the breeding site. No feeding occurs during this period (Cornish pers. comm.) and the migration characteristics have been studied by a number of researchers (see Chapter 1). Toads are more reclusive and highly sedentary during the post-breeding terrestrial phase (Oldham and Swan 1992) and activity may be restricted to only 11-22 suitable evenings over the summer period (Slater 1992). It was hypothesised that adult activity over the summer period would be characterised by short distance movements within a defined home range, but animals would take advantage of suitable evening conditions for foraging. Toads were followed throughout their summer period (May-October) using radio-tracking.

Specific objective: **To identify the role of micro-climate in toad activity.**

Several climatic cues are believed to influence the timing of toad migrations. The role of air temperature is evident with several studies reporting correlations between the number of toads observed and air temperature (Gittins, Parker and Slater 1980, Slater, Gittins and Harrison 1985, Fraser 1986, Denton and Beebee 1992, Grist 1994). A period where night temperatures are consistently above 6°C is considered the

threshold required for initiating the spring migration, although other factors such as day length, humidity and seasonal rhythms may also be influential (Wisniewiski, Paull and Slater 1981). It was hypothesised that toad activity would be governed by evening temperatures throughout the year, although the spring migrations would show greater dependence upon climatic cues than the activity patterns recorded during the summer. Climatic variables were collected throughout the year and compared to toad activity. Activity patterns were defined using pitfall trappings (number caught), radio-tracking (by the distance moved by individual animals) and by the number of toads seen active on each evening.

2.2.4 Habitat quality

Grading of habitats on the basis of the benefits they provide for the toad (reflected in individual survival, growth, body condition) allow comparison between habitats. This may help to explain the spatial distribution of a species on a geographical scale, and permit recommendations on the composition of landscapes for conservation management.

Specific objective: **To compare individual condition, growth and survival in contrasting habitats.**

The condition, growth and survival of juveniles and adults in contrasting habitats during the terrestrial period was compared through trapping data. The body condition of the toads, based on a ratio between mass and length (*sensu* Kuhn 1994) is cited as an indicator of habitat quality. It was hypothesised that toads in woodland and scrub habitats would show a faster growth rate, better condition and higher survivorship than individuals utilising arable habitats.

Specific objective: To evaluate the use of ecological parameters in defining habitat quality.

The elements of habitat density and the size of the home range, survival, female fecundity, somatic condition and individual body growth provide an assessment of the relative benefit of different habitats towards the success of the toad, therefore reflecting the suitability or quality of the habitat for toads. The value of each of these

factors as indicators for habitat quality for the toad was addressed in terms of the dynamics of the target population. In was hypothesised that female fecundity would be the most appropriate indicator of habitat quality, since females require resources for both egg production and to maintain body condition.

2.3 Approach to research

The aims and objectives have been approached through a combination of radio-tracking and field population studies. Radio-tracking techniques have been established over the past three decades (Mech 1980, Amlander and Mcdonald 1984, Priede and Swift 1992) to study a wide range of species, including amphibians (Nuland and Claus 1983, Olders, van Gelder, and Krammer 1985, Fukuyama *et al.* 1988, Sinsch 1988, Denton 1991, Seitz, Faller-Doepner and Reh, 1992, Oldham and Swan 1992). Similar field population studies, with annual movements monitored using a series of drift fences and pitfall traps, have been used successfully in other studies (Oldham 1966, Gibbons and Bennett 1974, Gittins 1983a, Oldham 1985, Swan 1986, Oldham and Swan 1991).

Chapter Three: Methods

3.1 Species selection

Amphibians are particularly well suited to ecological and population studies for a number of related reasons. First, their ease of capture in large numbers, particularly during the annual breeding season. Secondly, once captured adult amphibians may be relatively easily marked, permitting population studies based on mark recapture techniques. Thirdly, amphibians are relatively sedentary with small home-ranges (Chapter 1).

The common toad has additional characteristics that make it a more appropriate choice for the current study over other amphibian species, such as the crested newt (*Triturus cristatus*), natterjack toad (*Bufo calamita*) and common frog (*Rana temporaria*). The common toad is climatically adapted to colonise the whole of the British Isles and is fairly ubiquitous (Swan and Oldham 1989). However, unlike the common frog, the toad is a specialist that is believed to require a defined range of habitats for survival (Swan and Oldham 1993). In addition, the common toad is frequently recorded in the British countryside, exists in a variety of habitats (unlike the natterjack toad, and) in large populations (normally more than 500 adults) that are relatively sample (Oldham pers. comm.), making it easy to monitor (unlike the crested newt).

3.2 Life stages

For the benefit of the current study four life stages have been identified; the *tadpole* or *larval stage* representing the developmental period from egg to metamorphosis; the *metamorph* stage representing the period from emergence from the pond after metamorphosis, continuing until the first winter; the *juvenile* stage representing all individuals after their first winter that are not sexually mature (assumed to be less than three years of age for males and four years of age for females), and the *adult* stage representing all individuals that are sexually mature.

3.3 Research sites

Three study sites were used during the current study: Osbaston Hall, Leicestershire; Little Wittenham Nature Reserve, Oxfordshire; and the radio-tracking enclosure, Coleorton, Leicestershire.

Osbaston Hall was the primary site used for the current study, and the source of the data for the population studies. Osbaston Hall was selected as part of the JAEP study and an initial year of data had been collected before the commencement of the current study (Smithson 1991). The breeding site at Little Wittenham was surrounded by homogeneous blocks of woodland to a distance of 300m, providing a contrast to the arable dominated Osbaston Hall. The radio-tracking enclosure was constructed to be used in conjunction with the automated system (see Chapter 5 and French *et al.* 1992, Appendix 1).

3.3.1 Osbaston Hall, Leicestershire (SK 424046)

Osbaston Hall is a modern arable farm of 30 hectares located in north-west Leicestershire. The breeding site was surrounded by agricultural fields; but small fragments of semi-natural vegetation remained. During the current study, 70% of the estate was devoted to arable, Figure 3.1. The composition of the estate remained consistent, with the only major change being the conversion of a field to the north-west of the lake from grazing pasture to arable in 1991/2. This was not associated directly with any trap lines, although the field was adjacent to the western side of the Wood (WDI, WDO) enclosure. Two water bodies make up the breeding site; the lake (0.7ha) and the linear spur (0.2ha), Figures 3.2 and 3.3. The lake is fed from the east by a spring, with the spur fed by the overflow from the lake and draining to the south. On the western bank of the breeding site is a poplar plantation, Figure 3.4, dominated by an understorey of hogweed and nettles (1.9ha). To the south of the Spur is an area of mixed woodland, the Rookery, with frequent rose species and bramble and a ruderal understorey of nettle and willowherb (0.9ha), Figure 3.5. To the east and north of the Lake is an area of rough pasture (4ha), grazed in summers of 1991 and 1992 with horses and in 1993 and 1994 by cattle, Figure 3.6. To the north of the lake separated by rough grassland is a small broadleaf woodland copse (1.8ha) dominated by ash with an

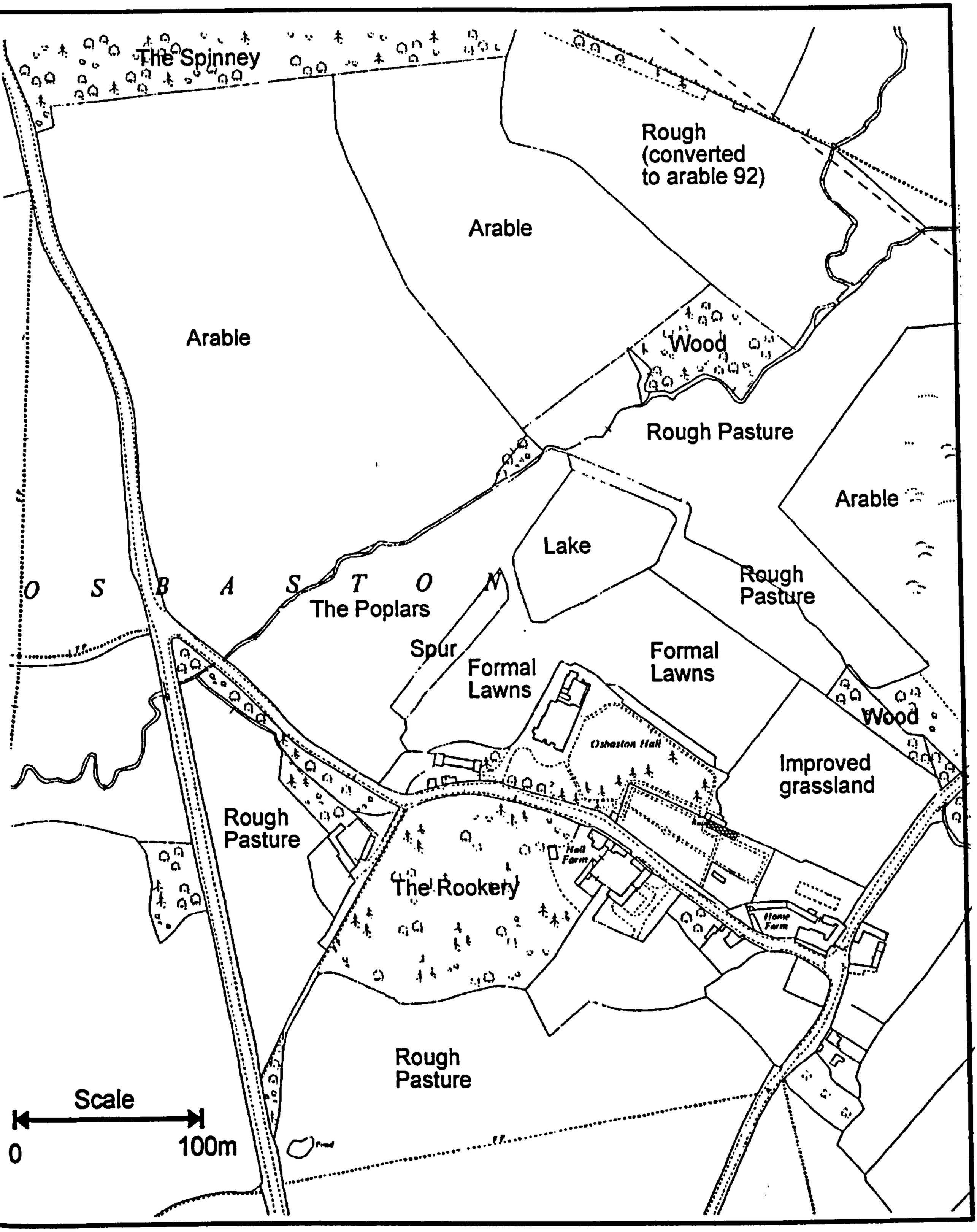

Figure 3.1: Osbaston Hall Estate, Leicetsershire showing main habitat types present, and location of the two water bodies that made up the breeding site.

Figure 3.2: View of Spur, Osbaston Hall, photographed from the Hall and facing the arable fields to the West. March 1994.

Figure 3.3: View of Lake, Osbaston Hall, photographed from the Hall and facing the arable fields to the West. March 1994.

Figure 3.4: Poplar Plantation photographed from the East bank of the Spur. The Poplar North fenced circle, made from black polythene sheeting, is visable in the centre of the photograph. March 1994.

Figure 3.5: Rookery showing ground flora dominated by ruderal herbs, e.g. nettles, willowherb, bramble with horsetail in the damper areas. April-May 1994.

understorey of bramble, Figure 3.7. On the western boundary of the estate, 450m from the breeding site is a strip of woodland, referred to as the Spinney. Hedgerows, dominated by hawthorn, separated the arable fields, pasture and connected the woodland blocks to the west and north of the breeding site. During the current study there was a rotation of rape, cereals, root crops, peas and linseed on the arable fields (21ha), Figure 3.8.

3.3.2 Little Wittenham Nature Reserve, Abingdon, Oxfordshire (SU 573927)

Little Wittenham, 12 miles south of Oxford, consists of 52 hectares of woodland surrounded by 49 hectares of permanent grassland grazed throughout the year by sheep, Figures 3.9 and 3.10. Two ponds exist in the middle of the wood, used by common frog, common toad, smooth newt and great crested newt (Duff 1989), Figures 3.11 and 3.12. Little Wittenham Wood had been centre of previous research (Duff 1989, Franklin 1993 and Latham *et al* 1996, see Appendix 2).

The wood consisted of areas of coppice, dominated by hazel, with areas of mixed woodland and conifer plantation. Woodland management, including the removal of conifers from the mixed woodland and re-instatement of coppice in parts of the wood was being undertaken throughout the period of the current study, although the woodland blocks that contained fences were unaffected.

3.3.3 Radio-tracking enclosure, Coleorton, Leicestershire (SK 396168)

The enclosure (846m^2) at Coleorton, used with the automated radio-tracking system (French *et al.* 1992, Appendix 1), was situated in a partly walled garden in a semi-rural landscape in north-west Leicestershire. A toad-proof fence was built around the enclosure in 1990. The garden was used by the common toad during its terrestrial phase and during migrations to and from the breeding site located 500 metres to the north (Oldham 1985, Oldham and Swan 1991).

Figure 3.6: Rough Pasture, Osbaston Hall. Photographed from the north, showing the north-east tip of the Lake. March 1994.

Figure 3.7: View of the Rough Pasture to the east of the lake showing the Wood copse to the North of the Lake, facing North-East. March 1994.

Figure 3.8: Arable West field with a crop of oil seed rape, photographed from the west towards the breeding site. The Poplar Plantation can be seen with the black polythene circle representing the Poplar North circular habitat specific enclosure. April 1994.

Figure 3.9: Two woodland blocks (deciduous woodlands to the left and coniferous plantation to the right) at Little Wittenham Nature Reserve, photographed from Church Meadow. March 1995.

Figure 3.10: Main habitat types at Little Wittenham Nature Reserve, Oxfordshire (from Franklin 1993).

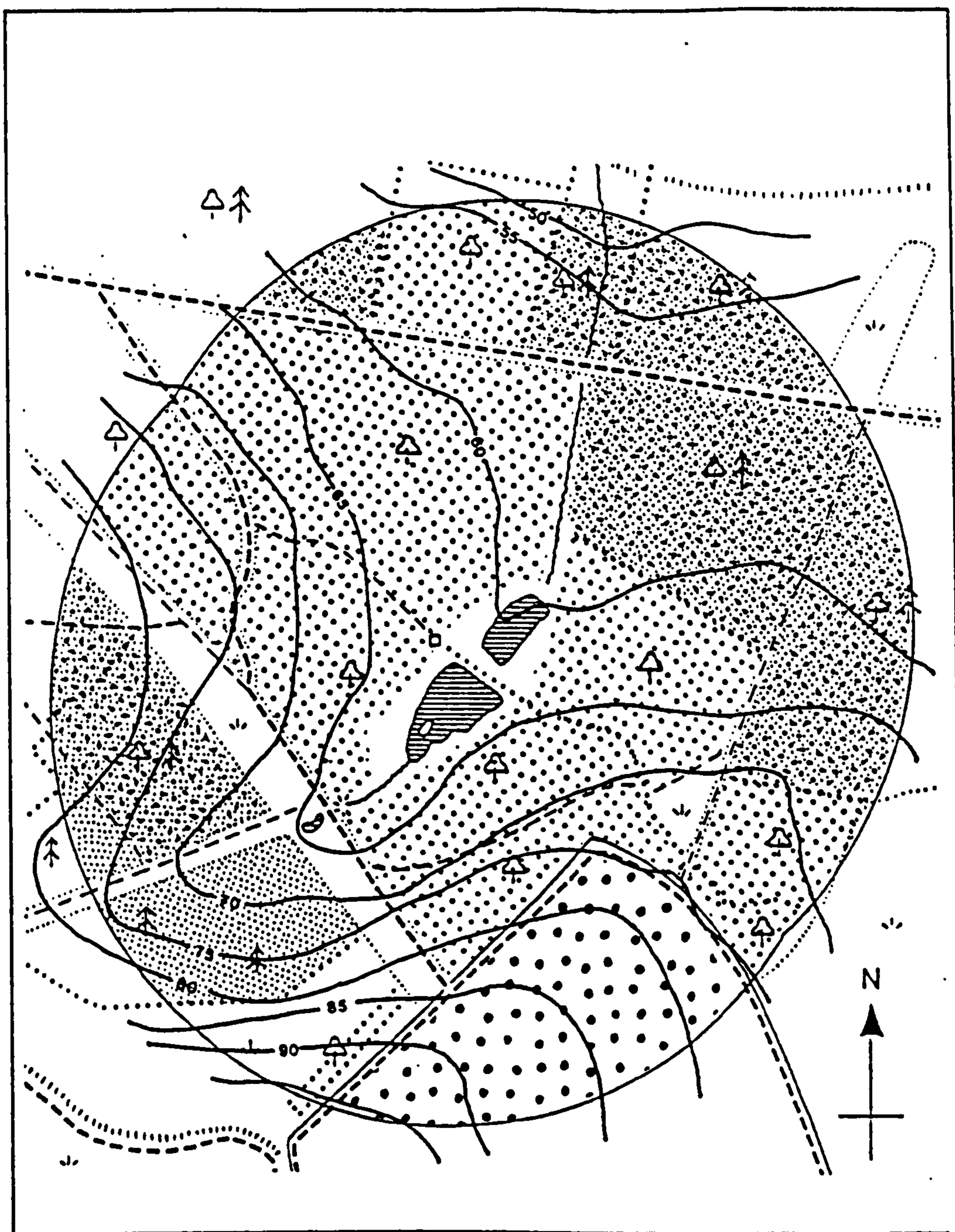

Figure 3.11: Top pond at Little Wittenham Nature Reserve. A short section of terrestrial drift fence can be seen middle left hand section of photograph. At LWNR chicken wire fences were covered in plastic sheeting and used as part of the studies on the population dynamics of the great crested newt. March 1995.

Figure 3.12: Bottom pond at Little Wittenham Nature Reserve, photographed from bank and toward the top pond (Figure 3.11). The banks had recently been cleared of large trees. A recently lopped tree can be seen in the foreground. March 1995.

3.4 Tagging

3.4.1 Toe-clipping and 'Panjet' marking

Two methods of marking individuals were used for animals captured during the breeding season; toe-clipping and 'Panjeting'. Under licence from the Home Office a single toe was removed from one of the four limbs. The thumb and first digit of the front limbs on the male were not removed, as these are used for clasping during amplexus. The longest digits on the hind limbs of both the female and male were untouched, as these were expected to have the most serious effect on mobility. Each toe was coded and used in conjunction with 14 potential Panjet locations. The 'Panjet' (originally a dental instrument used to apply anaesthetic) injects a small quantity of ink under high pressure into the skin to produce a small mark (Wisniewski *et al.* 1981). Panjet marking, in conjunction with a toe-clip, permitted each animal to receive a tag indicating the year of capture and location without the need to amputate more than one digit.

On recapture no further toes were clipped, although a new Panjet mark was given. Whilst toe-clipping in the common toad produces a permanent mark, since digits do not regenerate as in some newt and salamander species, the Panjet mark was not always permanent, but did permit identification from one year to the next.

3.4.2 Insertion of radio-transmitters

Toads were force fed radio-transmitters, sized 16mm x 9mm x 6mm and supplied by Biotrack (Stoborough, Wareham, Dorest, UK). The mouth of the toad was gently opened with an index card and the tag pushed down the throat; the sinking of the eye balls indicated that the tag had been swallowed (Oldham and Swan 1992). Transmitters remained in the stomachs of the toads until they were regurgitated, since they were too large to pass the pylorus. The number of days the tags retained in the stomachs of males (mass range 18 - 35g) ranged from 2-38 days (with a median of 15 days) and 2- 38 days (with a median of 13 days) for females (mass range 17 - 88g).

3.5 Breeding migrations: Method descriptions

Three methods of monitoring were used during the breeding season (1991-1994) to record animal movements and to estimate the size of the adult population: night-counts of animals in the water body, a mark, release and recapture exercise (MRR) and interception fences and pitfall traps. In the current study a MRR was completed at Osbaston in 1992 and 1993 and at Little Wittenham Nature Reserve in 1995.

3.5.1 Water body counts

Counts were made, on a nightly basis, of the number of toads present in each water body at Osbaston Hall between 22:00 hrs. and 00:00 hrs. during the breeding seasons of 1991-1994. Night counts of breeding individuals have been recommended to determining site value in establishing biological SSSIs (NCC 1989). Regular counts started once the first dozen animals were observed in the water and concluded once the last new spawn was observed (Cooke and Oldham 1995). During night counts the numbers of single males and pairs in amplexus were recorded in each of the water bodies by scanning the water during a slow walking pace using a hand torch. For the west bank of the Spur (SW) and the west and east banks of the Lake (LW and LE), the total numbers of single males and pairs on and below the water surface were recorded, Figure 3.13. Data from earlier studies on site in 1990 (Smithson 1991) identified the western side of the spur and both the western and eastern sides of the lake as the main areas for activity; only these three banks were studied in depth during subsequent years (1991-1994). Climatic variables (air and water temperature and relative humidity) were recorded in 1992-94 on the western bank of the breeding site on arrival (c. 20:00 hrs.) using a wet/dry whirling hygrometer (Casella) and a mercury thermometer placed vertically in the top 10cms. of the pond.

Some attempt to provide a measure of the precision of the counts was undertaken by ensuring that a second count was made by the research supervisor on occasional nights and the results were compared. The success of the water body counts in determining the size of the breeding population was evaluated using a mark, release, recapture model and is discussed later.

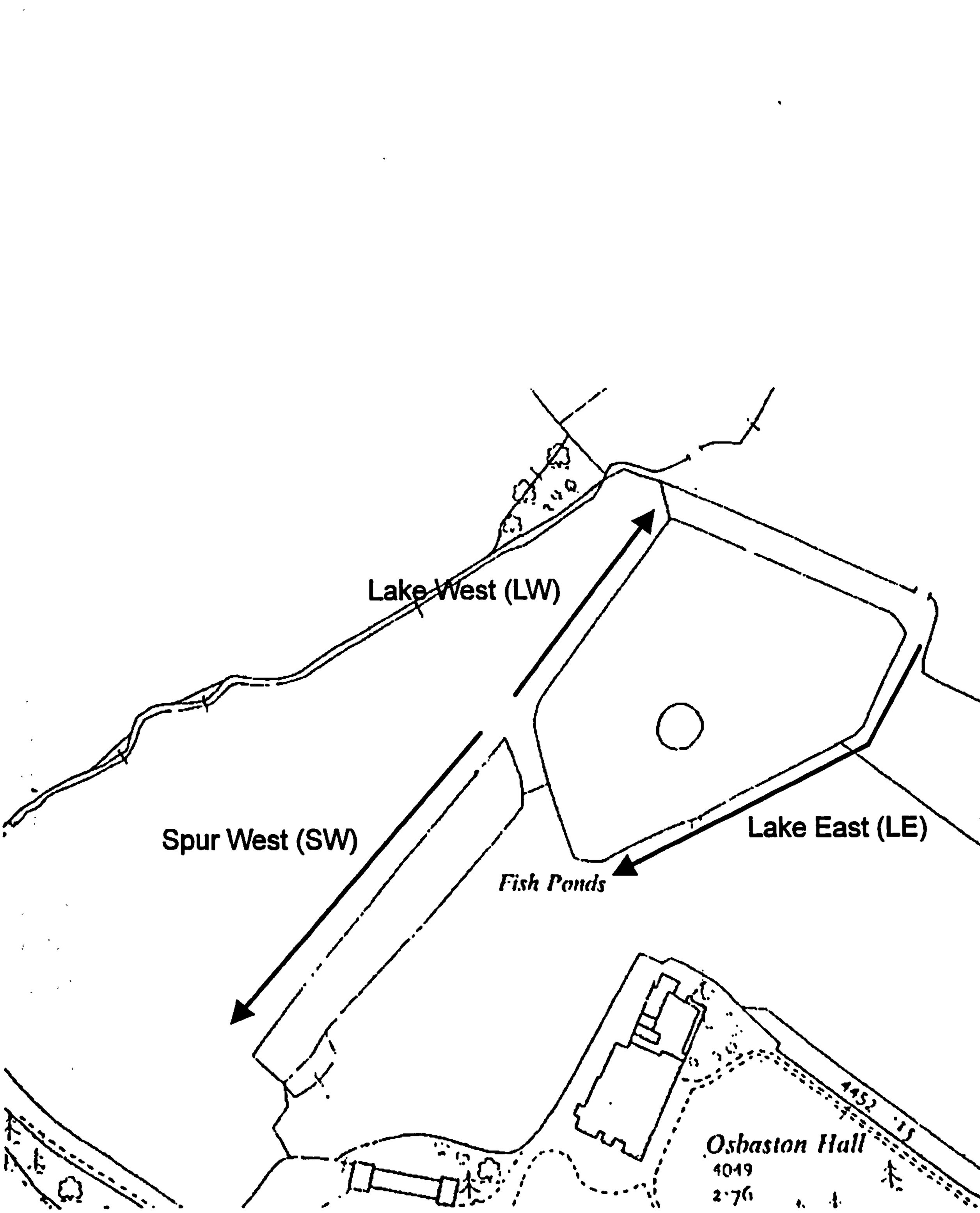

Figure 3.13: Breeding site at Osbaston, showing the subdivision of the two water bodies and the walking direction during the night counts.

3.5.2 Mark, release, recapture exercise

The size of the adult male population at both Osbaston Hall (1992 1993) and Little Wittenham (1995) was estimated using Jolly's mark, release and recapture method (Blower, Cook and Bishop 1981) during the breeding season.

Capture-recapture models make three basic assumptions:

1. Marked and unmarked animals are captured randomly;
2. Marked animals are subject to the same mortality rate as those unmarked;
3. Marks are not lost or overlooked.

In addition to these there is the assumption that marked animals are not lost from the population through emigration and that the input of new animals into the population through immigration is also low. Given that the MRR exercise was conducted over the relatively short breeding period, it was felt that these influence of these potential discrepancies would be minimal. Female toads leave the water once they have spawned, and thus their chances of recapture are reduced compared with males. This violates the basic assumptions for the mark and recapture model, and for this reason only the population of adult males was estimated. The female population size was calculated using the sex ratio of the data obtained from the pitfall catches, since these data would not have the same temporal bias.

Toad numbers, as determined by night counts, at the Osbaston Hall and Little Wittenham breeding site were recorded each evening, once the count had risen to the region of 50 animals the first collection of animals took place. On capture all toads were toe clipped, to indicate that the animal was part of the MRR, and given a Panjet mark representing the catch day (i.e. Day 1), then released. A night count was completed on the following night, but no collection made. On the third night of the exercise a count was completed with a second batch of animals collected *after* the count. These animals were divided into new animals (i.e. untagged) and

recaptures[1]. For the recaptures, the number of toads with tag representing Day 1 mark was recorded. All animals were then toe clipped as with Day 1, but given a Panjet mark in a different location (representing Catch Day 2).

For Osbaston Hall, this process was continued over a period of five days, with three collection days (Day 1, Day 2, Day 3), during the 1992 and 1993 breeding seasons. At Little Wittenham in 1995, the number of toads counted at the breeding site continued to increase during the exercise, and it therefore lasted 11 days, representing six collection days. The adult population size was calculated by analysis of the proportion of marked and unmarked animals (*sensu* Blower, Cook and Bishop 1981).

3.5.3 Pitfall traps, drift fences and habitat specific enclosures

Fences were constructed from 1.3cm (0.5 inch) gauge chicken wire. The base of the wire was placed into a 10cm trench in the ground and bent flat with the bottom of the trench, to prevent animals finding a way underneath the fence. The trench was back filled with earth to hold the fence secure. The chicken wire was held vertical and tacked to wooden posts, provided at 10m intervals, using galvanised staples. Ten-litre plastic buckets were dug at 10m intervals for pitfall traps. These pitfalls were set flush with the ground and tangential to the fence; a tight fit was required between pitfalls and fence to prevent the toads evading the trap. This was achieved by securing the wire beneath the lip of the bucket. The pitfalls were filled with water to a depth of 10cm to prevent desiccation of animals, provide cover from potential predators and reduce the chances of escape. If pitfalls were placed in flooded areas they tended to be forced upwards by hydrostatic pressure and were held in place by heavy duty tent pegs. The final height of the fence was about 40cm. An overhang of 10cm at the top of the fence was made in the opposite direction to the anticipated migration to prevent animals from scaling the

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[1] There were examples when animals caught during the MRR exercise possessed tags specific to terrestrial locations; for the benefit of this estimation these tags were ignored and these animals were treated as new individuals, unless they exhibited an addition tag indicating a specific MRR mark.

fence. For greater detail on fence design see Arntzen, Oldham and Latham (1995), Appendix 3.

Drift fences were linear in nature and constructed on the boundary between contrasting habitats, to intercept toads moving in from adjacent areas. Drift fences have been used extensively in amphibian research (see Arntzen, Oldham and Latham 1995, Appendix 3 for review and listings). Habitat specific enclosures (HSEs) were constructed to enclose a particular feature or habitat, or where circular in nature. Fences were constructed and made 'toad-proof' during the late summer, and therefore these fences were used to estimate summer density in each habitat. Circular enclosures have been used previously by Oldham (1966, 1967) in population studies in North America.

Most movement by the common toad during the breeding season occurs at night therefore an early morning collection was required. Daily monitoring of the fences and pitfall traps occurred during the peak periods of movement. The fences required routine maintenance during monitoring, including removal of debris along the fence and inside the traps, changing of rancid water, replacement of broken buckets and fence repair. Animals were collected from site and weighed and measured in the laboratory. All animals were released at a location close to their point of capture, but on the opposite side of the fence at which they were captured.

3.5.3.1 Interception fences: Osbaston Hall (1992-94)

The location of the drift fences and HSEs over the course of the current study are shown in Figure 3.14a-3.14c and as described below. Drift fences were constructed on the distal (referred to the Spinney) and proximal (referred to as Arable West) boundary of an arable field to the west of the breeding site. These fences were each 100m in length with 10 pitfall traps placed on the distal side of the fence. The woodland copse to the north of the lake was completed enclosed by a 380m toad fence (1992 only) with 28 pitfalls on the inside and 15 pitfalls on the outside forming the largest HSEs constructed at Osbaston Hall. The hedgerow to the east of the breeding site was enclosed and sub-divided into three continuous sections (1992-1994); Hedge East, Hedge Central and Hedge North. This hedge enclosure

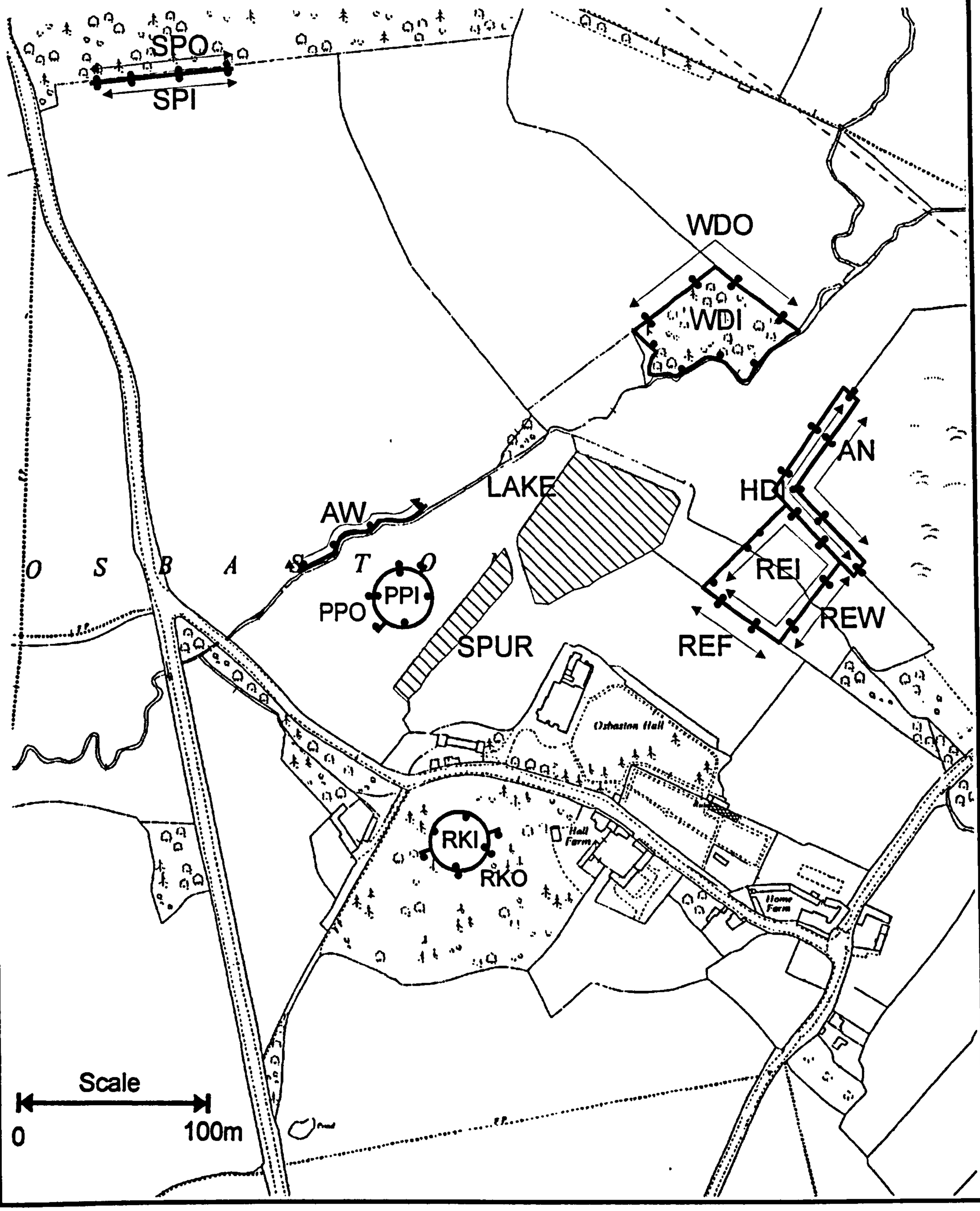


Figure 3.14a: Fence locations at Osbaston Hall during the breeding season of 1992. The location and number of pitfall traps is for illustration only.

Habitat specific enclosures (HSE), see Table 6.1 (Chapter 6) for codes

Drift fences (not to scale), see Table 6.1 (Chapter 6)for codes

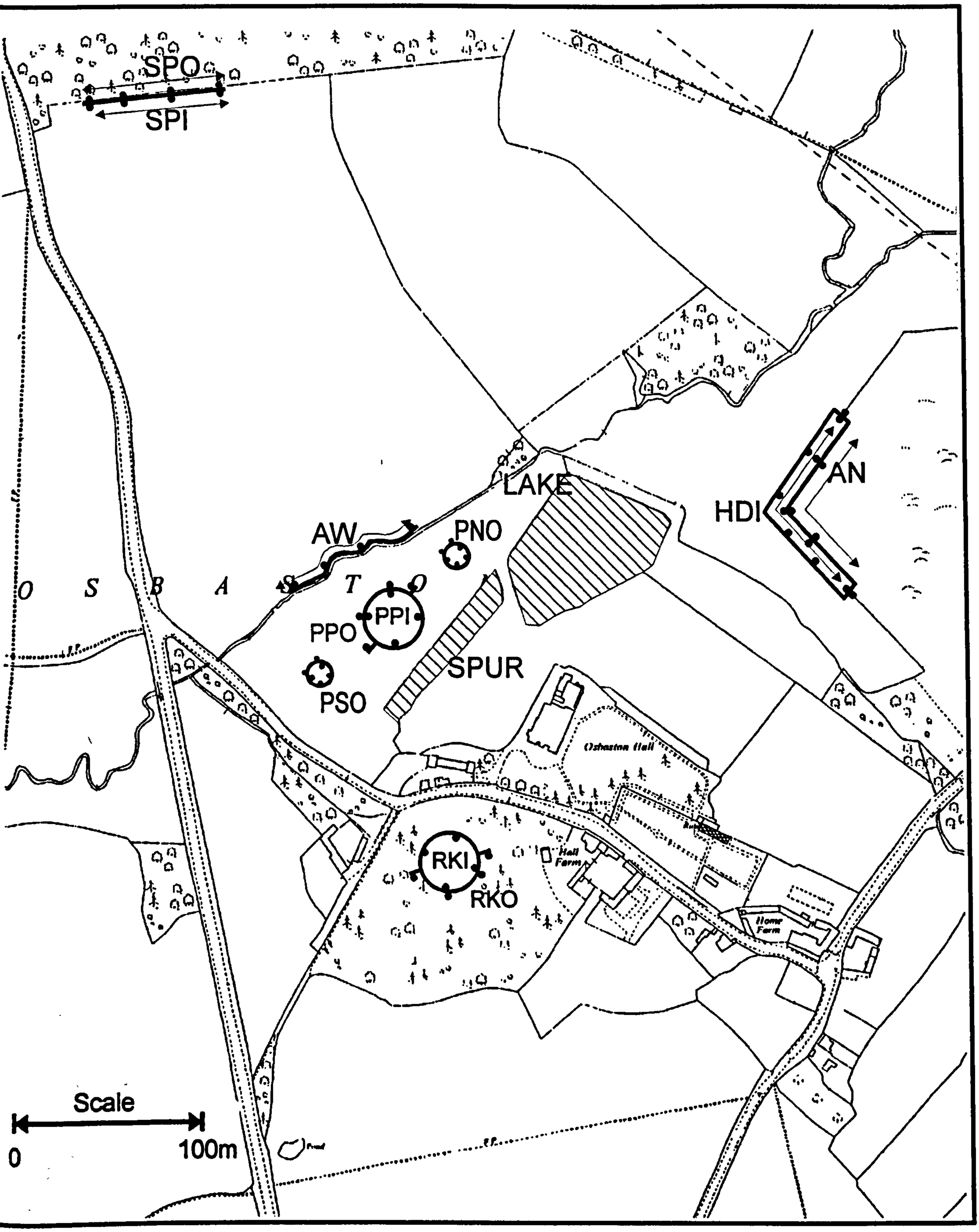


Figure 3.14b: Fence locations at Osbaston Hall during the breeding season of 1993. The location and number of pitfall traps is for illustration only.

Habitat specific enclosures (HSE), see Table 6.1 (Chapter 6) for codes

Drift fences (not to scale), see Table 6.1 (Chapter 6)for codes

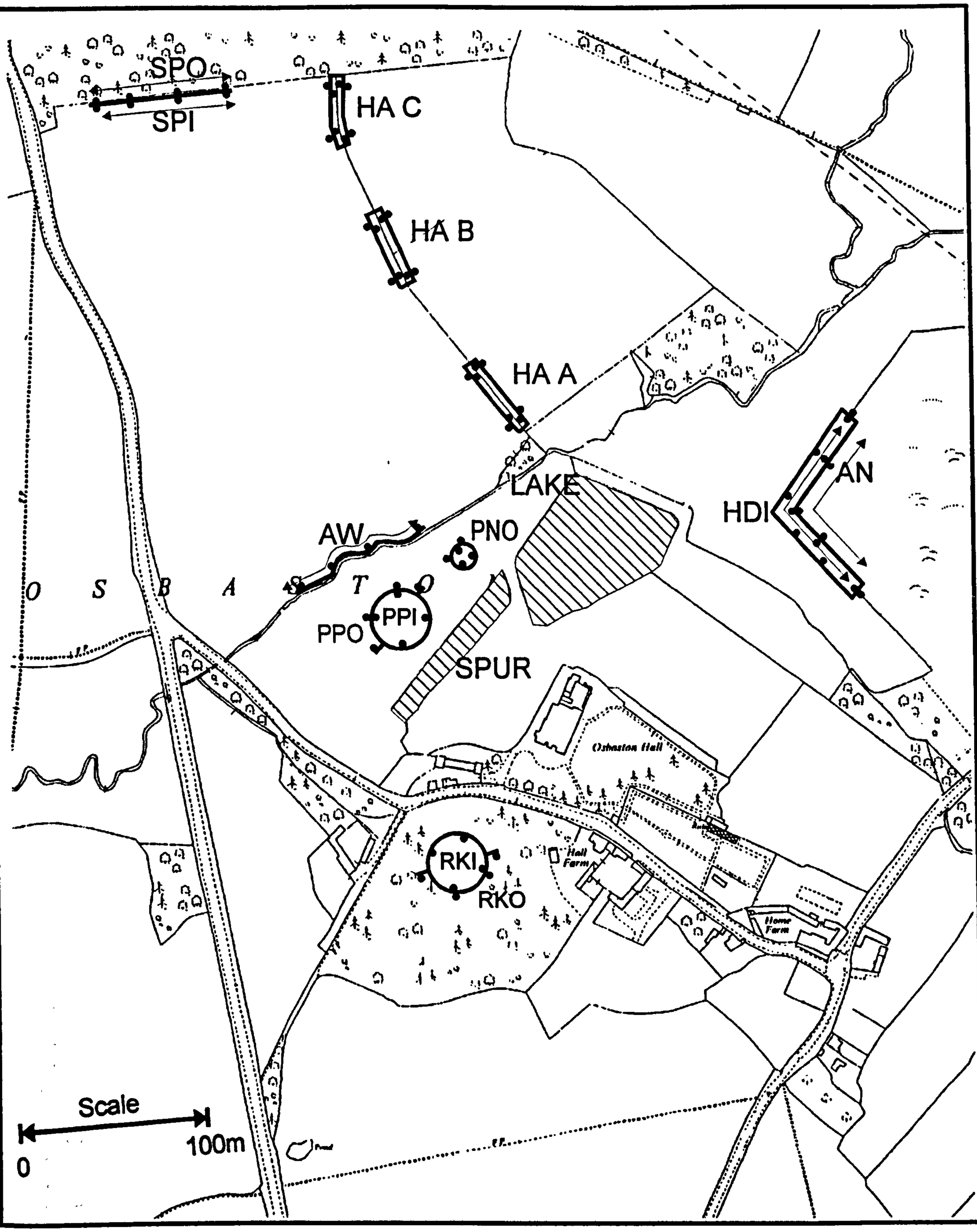
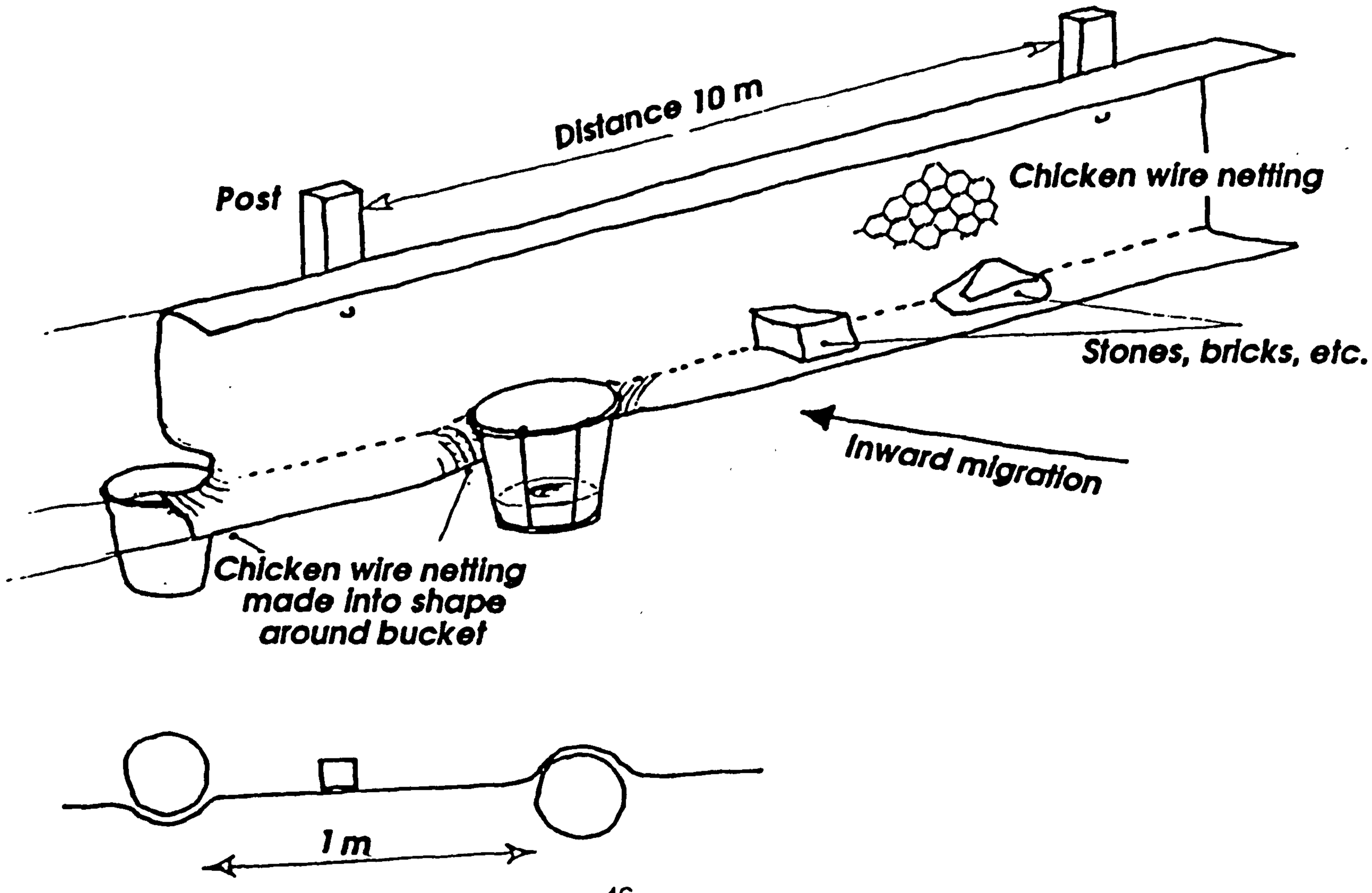


Figure 3.14c: Fence locations at Osbaston Hall during the breeding season of 1994. The location and number of pitfall traps is for illustration only.

Habitat specific enclosures (HSE), see Table 6.1 (Chapter 6) for codes

Drift fences (not to scale), see Table 6.1 (Chapter 6)for codes

Figure 3.15: Schematic representation of a chicken wire fence/pitfall system for toads as used at Osbaston Hall (after Arntzen, Oldham and Latham 1995)



was linked to a series of drift fences that formed an enclosure referred to as the Rough East complex (1992 only). The Rough East complex consisted of an area of rough pasture with its boundaries surrounded by an improved grassland to the south and a small copse to the east. Single circular HSEs were constructed in the Poplars and Rookery and maintained throughout the study (1992-1994). Each had a radius of 30m (198m circumference), with 20 pitfalls placed equidistant on the inside of the enclosure with 12 on the outside, Figure 3.15. The circular enclosures at Osbaston Hall were designed with a short 2m arm at opposite polar positions on the outside edge of each fence; these were intended to increase the trapping area for toads moving in from the west. In the autumns of 1991 and 1992 the HSEs in the Poplars and Rookery, the Wood (1991 only) and the hedge to the east of the breeding site were re-constructed (i.e. made toad-proof). The catches in the following spring would therefore represent summer animal densities.

Whilst the HSEs in the Poplars and Rookery; the drift fences at the Spinney, arable west and arable north; and the hedge enclosure (rough east) were maintained in each study year during the current study (1991-1994), Figures 3.14a-3.14c, the Rough East complex could not be constructed in 1993 or 1994 due to cattle grazing and the Wood enclosure was only functional in 1992. Additional fences included two smaller circular enclosures (12 metre radius), constructed in the Poplars as part of fence efficiency trials (1993 and 1994) and the hedgerow to the west of breeding site, running up towards the Spinney, which was divided into three sections, referred to as Hedge Arable A, B and C (1994 only).

All fences were functional to trap toads by 1 March. Details regarding the functional periods of the fences are provided in Table 3.1 and fence descriptions are provided in Appendix 4.

3.5.3.2 Interception fences: Little Wittenham Nature Reserve

Four circular HSEs were constructed in broadleaf woodland with a single drift fence at the edge of the compartment at distances of 25, 100, 175 and 250 metres from the two breeding ponds. Three matching enclosures were constructed in a coniferous stand at distances of 25, 100 and 175 metres with a similar drift fence,

TABLE 3.1: Codes, description and operational period for toad fences used at Osbaston Hall, 1992-94.

Fence line	Code	Style	Function years	Fence length	Number of pitfalls
Spinney	SP	Drift	1992-94	100	10
Arable West	AW	Drift	1992-94	100	10
Arable North	AN	HSE	1992-94	150	13
Rough Wood	REW		1992	70	11
Rough Field	REF		1992	80	5
Rough Inner	REI		1992	80	27
Hedge Arable/Rough	HDI		1992-94	150	30
Rookery (inside)	RKI	HSE	1992-94	200	20
Rookery (outside)	RKO		1992-94	100	12
Poplar Central (inside)	PPI	HSE	1994-94	200	20
Poplar Central (outside)	PPO		1992-94	100	12
Poplar North (inside)	PNI	HSE	1993-94	60	6
Poplar North (outside)	PNO		1993-94	30	3
Poplar South (inside)	PSI	HSE	1993	60	6
Poplar South (outside)	PSO		1993	30	3
Wood (inside)	WDI	HSE	1992	210	28
Wood (outside)	WDO		1992	210	15
Hedge Arable (inside) A	HAI A	HSE	1994	100	10
Hedge Arable (outside) A	HA0 A		1994	100	10
Hedge Arable (inside) B	HAI B	HSE	1994	100	10
Hedge Arable (outside) B	HA0 B		1994	100	10
Hedge Arable (inside) C	HAI C	HSE	1994	100	10
Hedge Arable (outside) C	HA0 C		1994	100	10

Figures 3.16 and 3.17. Each enclosure was 200m^2 (8m radius) with six equidistant traps inside and three outside traps to intercept incoming animals.

The function of the HSEs was the same as at Osbaston, however the fence design was slightly altered to permit trapping of newts besides frogs and toads (Latham *et al.* 1996). This involved covering the chicken wire frame with plastic sheeting (temporary dampcourse material), gathered at the base, pulled taught and held in place by bending the chicken wire over placing the base of the fence in a 15cm trench and back-filling with the excavated earth. Pitfalls and posts were constructed as previously. Fences were constructed during February in 1994 and 1995 and monitored as at Osbaston Hall.

3.5.3.3 Interception fences: Fence efficiency

During each breeding season marked toads were released inside the various habitat enclosures at both Osbaston Hall and Little Wittenham to evaluate fence efficiency. Fence efficiency was defined as the percentage of marked toads released inside the enclosure that were recaptured in the traps on the inside. It was assumed that those toads not caught in the inside traps had evaded the fence.

Swan (1986) constructed chicken wire fences bent into an 'S'-shape, in an attempt to prevent fence trespassing in either direction. Fence efficiency for her study was estimated as 66%[2], other efficiencies are reviewed in Arntzen, Oldham and Latham (1995). As described previously, fence design at Osbaston included an overhang to prevent toads scaling the fence. During the current study other styles of fence design were used to improve efficiency. The two smaller enclosures (Poplar North and Poplar South) were constructed in 1993 with an additional piece of chicken wire fixed to the top of the existing fence to form a "T" shape in profile. In 1994 Poplar North was covered in polythene sheeting to replicate the design at Little Wittenham. During the period 1992-1994 the design of the original circle Osbaston

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[2] In this example fence efficiency was defined as the percentage of the total population approaching the fence that is caught in the pitfalls. This estimate was inappropriate at Osbaston since there was no perimeter fence

Figure 3.16: Circular habitat specific enclosure (HSE) located in the former coppice compartment, Little Wittenham Nature Reserve. The circumference of the HSE was 50m. March 1995.

Figure 3.17: Circular habitat specific enclosure (HSE) located in coniferous plantation, Little Wittenham Nature Reserve. The circumference of the HSE was 50m. March 1995.

Hall was unchanged, to provided a comparison between the efficiencies of alternative fence designs.

3.6 Adult summer movements: Method descriptions

The post-breeding movements were studied through a combination of night searches and radio-tracking.

3.6.1 Night searches

During each summer of 1992-94, night searches were made throughout the habitats and along the roads at the Osbaston Hall. These were completed by slowly walking through the Poplars, Rough East, the Rookery and along the field boundaries at Arable West and shining a torch in sweeps to the left and right. Attempts were made to ensure that a similar time was spent in each habitat. The aim was to find as many toads as possible, since these studies were conducted in association with other projects. Toads seen where collected and location noted. Temperature and humidity measurements were recorded using a wet/dry whirling hygrometer in the centre of each habitat during each evening's search.

3.6.2 Radio-tracking

In 1992 and 1994 adult toads were collected during the breeding migration, for use in summer radio-tracking studies, some animals were also found during the night searches. All animals were collected and stored in glass tanks until required, with every effort to ensure that they were kept in good health and that animals collected from different localities were kept separate. The time the animals were held varied between given circumstances (range 0 - 35 days). Each animal was weighed and measured on capture and before release. Previous tags were noted. Any untagged animals were tagged using a toe clip and Panjet on release.

Only animals with a body length greater than 50.0mm were used for the radio-tracking studies, since experience had indicated that animals below this size regurgitated the tag after only a short period (Oldham and Swan 1992). Both male and female animals were tracked in 1992, however, only female toads were released in 1994. The use of only females was an attempt to remove any variation

in habitat selection that may exist between the sexes; given the low number of animals that could be successfully tracked by a single researcher during a single season, the aim to was ensure a sample that was as large as possible that was as uniform as possible. The larger size of the females was beneficial to tagging since research had indicated a positive correlation between the tag retention time and individual length.

3.6.2.1 Radio-tracking: Automated tracking studies, May-October 1992

During May-October 1992, twenty-six toads were tagged with radio-transmitters and released into the enclosure at Coleorton. All toads were released into the centre of the enclosure to ensure equal access to all available habitats. The exact movement of these animals was followed using the automated radio-tracking system (French *et al.* 1992). The automated system was programmed to start tracking the toads from 20:00 hrs. each evening and continued until 6:00 hrs. the following morning. All details were written to a floppy disk that was changed once a week. Details of system function are described in Chapter 5.

3.6.2.2 Radio-tracking: Osbaston Hall, May-September 1994

During May-September 1994, 24 radio-tagged female toads were released at Osbaston Hall and their movements following by hand using a Mariner M-57 receiver (Mariner Radar, Campsheath, Lowestoft, Suffolk, UK). Twelve toads were released into the Rookery and 12 released into the arable field to the west of the breeding site. The Rookery animals were released into the centre of the Rookery, while the arable animals were released at the base of the hedge to the west of the breeding site. During radio-tracking, study animals were located once every hour during each study evening. Animals were located by following the bearings obtained by hand-tracking until the toad was seen (if active) or its refugium was located. Every effort was made to ensure toads were not disturbed. Tracking started around 22:00 on each evening. Tracking was abandoned if toad movement had not occurred by 3:00.

3.7 Metamorph output

The metamorph output at Osbaston Hall was measured during July-September 1991-1994. The exact sampling period was adjusted each year according to observations made on the development of the tadpoles. Metamorphs were caught in traps placed on the bank of each breeding pond as they emerged from the breeding site The trap consisted of a 'pot noodle' container placed inside a plastic beaker that had its base removed. The beaker provided the structure with addition strength, and allowed the pot noodle pot to be removed without disturbing the surrounding earth. A small hole was drilled in the side of the 'pot noodle' container to drain excess water after rainfall. The traps were set flush with the ground at 6m intervals around the perimeter of the Lake and the Spur. The trap was filled with 100ml of 0.1% solution of ethyl p-aminobenzoate (EpA) used as a narcotic. Monitoring was completed on a daily basis, when all animals caught in the pots were collected, the pots were cleaned and the EpA solution changed. On collection all metamorphs were stored in 10% formaldehyde solution.

In 1993, a line of 20 traps was placed on the edge of the wheat field (Arable West) to the west of the breeding ponds and a similar line placed 150m further west close to the edge of the Spinney. These traps were placed 15m apart, but constructed in an identical fashion to those placed on the perimeter of the breeding ponds.

In the laboratory metamorphs were patted dry with tissue paper and weighed to an accuracy of 0.001g. Each metamorph was grouped into one of five groups dependent upon the level of tail reabsorption. Group five represented animals where the tail was visible and showed only limited signs of reabsorption, group four represented animals where some reabsorption was evident, group three represented an extended stump, group two a stump, group one represented almost complete reabsorption. Where the tail had been completely reabsorbed and only the tail bud remained animals were graded as 0. This grading was to ensure that catches were compared using animals at the same stage of development.

Total emergence is defined as the estimated number of metamorphs leaving the breeding site based on an extrapolation from the gross metamorph catch. This

extrapolation uses the total 'sampling length', defined as the sum of the widths of each trap, and the perimeter length of each breeding pond. This ratio was then used to extrapolate the gross metamorph catch to the total emergence; the variation in catch between traps was used to provide a confidence interval.

3.8 Toad morphometrics

3.8.1 Body length and mass

Body length (referred to as DLU) was measured from snout to the posterior of the urostyle (Breckenridge and Tester 1961) to the nearest 0.5mm. A steel rule, with a metal stop riveted at the start of the calibrations, was held against the urostyle and pressed along the toad's backbone. Length was recorded from the tip of the snout to the base of the urostyle. The urostyle forms a consistent point for measurement but is only firm in animals larger than 35mm (Oldham pers. comm.). Mass for each animal was recorded to the nearest 0.1g using an electronic balance.

3.8.2 Sex

Toads were sexed by the presence (males) or absence (females or juveniles) of nuptial pads on the inner digits of the front feet of males. Females were classified further as gravid, or having shed their eggs. Juveniles were noted as males or females only if they illustrated distinctive characteristics (colouration, body shape).

3.8.3 Body condition

The following ratio between mass and body length, was used to provided a measure of condition for the common toad, Equation 3.1.

$$Condition = \frac{mass}{length^3} * 10^6$$

Equation 3.1

Where: Body mass is the full hydrated mass (g); Length is the snout to urostyle dorsal length to the nearest 0.5mm. The ratio is multiplied for convenience (Kuhn 1994).

3.8.4 Fecundity

Fecundity was estimated by counting the number of eggs produced by a single female. Some females were collected from the traps at the drift fences or within the HSEs and paired with males. Existing pairs were also removed from the breeding pond. All pairs were placed into 10 litre plastic buckets, containing 15cm of water and laying material (usually watercress) and allowed to spawn. The spawn was separated from the laying material, drained and stored in 10% formaldehyde solution for later reference.

If female corpses were found on the roads surrounding the breeding site, these were dissected and the ovaries preserved in the same manner as the eggs. After leaving to dry in the air, the ovaries could be more easily dissected and the number of eggs counted in the same manner as the spawn.

3.8.5 Age

Skeletochronology has been used for many age studies in amphibians (Hemelaar and van Gelder 1980, Gittins, Steeds and Williams 1982, Gibbons and McCarthy 1983, Halliday and Verrell 1988, Augert and Joly 1992, Johnson 1992). The technique is based on the observation that bone growth is periodic. Reduced growth during the winter months produces a characteristic ring when the bone is stained with a haematoxylin, therefore, age is reflected by the number of growth lines or rings. Concern may be directed to this method due to the resorption of lines leading to errors in individual age determination (Smirina 1983). Although each toe was visual checked for evidence of resorption, no other method has used to judge the degree of resorption, for example the study of metamorphs (sensu Hemelaar 1986). However, a previous study in the region showed little evidence of resorption (Johnson 1992) and research by (Hemelaar 1986 and Paton *et al.* 1991) suggests that the frequency of resorption may depend more on geography than on taxonomy.

The method used in the current study was based on Hemelaar and van Gelder (1980) and adapted by Johnson (1992). The toes that had been removed from

Osbaston Hall toads (1990-1994) for marking were saved for age analysis and frozen in tap water until required.

After thawing, the phalanges were boiled in tap water until the skin and any muscle tissue could be striped from the bone. The phalanx was then decalcified in a solution of 5% formic acid until softened, usually for at least one hour. The acid was removed from the sample by rinsing in tap water. Most samples were used immediately after decalcification, however the prepared bone could be stored in tap water in a fridge (c. 5°C) for a maximum of two weeks. For longer storage samples required fixing in 70% alcohol followed by rehydration before sectioning (Johnson 1992). The phalanges were freeze-mounted onto a metal cryostat chuck using a small amount of O.C.T. compound (Gurr, product number 36160) using liquid nitrogen. The phalanx was inserted into the compound and fixed, as perpendicular to the chuck as possible, then sealed with O.C.T. The chuck was then placed inside the cryostat and allowed to warm to chamber temperature (set at -30°C). Transverse sections of eight microns thick were taken and transferred from the blade to a cover slip for staining.

The sections were stained by immersion in a bath of haematoxylin stain. Originally Delafield's haematoxylin had been used, however, this became unavailable and was replaced by Harris haematoxylin; this required a longer stain period (5-8 minutes rather than 2 minutes for Delafield's). The racks were then placed in clean tap water to remove any excess stain. After rinsing, the cover slides were mounted on to prepared slides using glycerine jelly mountant. All slides were then photographed at x100 magnification, since the haematoxylin (particularly the Harris haematoxylin) faded within a few weeks of staining. In the current study, the samples were collected during the breeding season, and therefore the outer margin of the bone section was considered the final ring since the animals had just come out of the over-wintering period, see Figure 3.18

Figure 3.18: Haematoxylin stained bone section at 100x magnification. Four lines can be seen in the section, indicating four over-wintering periods. Since the animals were collected during the breeding season, the outer margin of the section is considered as the final line. This individual was therefore estimated to be five years of age.

3.9 Growth

3.9.1 Adult growth

Although a combination of toe-clipping and Panjet marks were used, animals were not uniquely marked. Therefore adult growth could only be based on a group basis and was estimated by comparison of the size of new individual (ie untagged) and recaptures in each habitat, i.e. growth in the Poplars was calculated by comparison on 1991 new individuals and 1992 Poplar recaptures.

3.9.2 Comparative growth rates of juveniles in contrasting habitats

During the period 3 June to 10 October 1994 the growth rate of juveniles placed in $6m^2$ enclosures in the Rookery and the Poplars was monitored in a replicated experiment. The enclosures were built to permit the movement of invertebrates into the enclosure, but prevent escape of the juveniles. The fences were constructed using a chicken wire frame covered to a height of 30cm with 'Netlon'. The base of the fence was buried in the ground with a lip to prevent breaching of the fence by burrowing mammals, Figure 3.19. Plastic sheeting was stapled above the Netlon and secured at the top of the fence, Figure 3.20. Total fence height was 60cm.

Forty juveniles, ranging in mass from 1.1 to 6.4g, were grouped into four sets. The combined mass of the four groups was not significantly different at the start of the experiment. All juveniles above 2.5g were toe-clipped, those less than 2.5g were considered to be too small to tag without affecting their survival. Six roof tiles were placed inside the enclosures to help capture. Tiles have been used as artificial refugia by toads (Denton and Beebee 1992) and appear particularly effective for juveniles (Cornish pers comm.). Enclosures were searched every 6-7 days and the juveniles were weighed and returned.

3.9.3 Growth after metamorphosis

Post-metamorphosis growth was estimated for 1993 by comparison of the length and mass measurements at emergence, at the Arable West traps and the Spinney traps.

Figure 3.19: Juvenile enclosure, Rookery, Osbaston Hall. The chicken wire was placed in a 50cm trench with a strip of 'Netlon'. The Netlon base of the fence was intended to permit the movement of invertebrates into the enclosure, providing a continuous source of prey for the juveniles but preventing their escape. June 1994.

Figure 3.20: Juvenile enclosure, Rookery, Osbaston Hall. The plastic sheeting was stapled to the Netlon, which was in turn was stapled into place at the top of the fence. The top of the fence was bent inwards to prevent escape. Final height was 30cm. June 1994.

3.10 Individual survival (inter-year)

Survival was calculated for each habitat using the number of individuals marked, for example in 1991, and re-captured in subsequent years. This method of survival estimation assumes that there is an equal chance of capture in all habitats in any one year and in the subsequent years.

3.11 Vegetation analysis

The habitats at Osbaston Hall and Coleorton were surveyed using an adapted version of the National Vegetation Classification in June 1991. Five quadrat locations were randomly selected in each habitat and the abundance of all vascular plant species was measured using the Domin scale. In all habitats, a 1m x 1m quadrat was used, except in the woodlands. In the woodlands, woody species were surveyed using a quadrat scale of 25m x 25m and non-woody species using a m x m quadrat.

The structure of each habitat was evaluated by measurement of the total vegetation cover. Cover was visually estimated at 5 levels 0-10 cm, 10-100 cm, 1-5 m, 5-10 m and above 10m.

3.12 Habitat selection, utilisation and patterns of activity

Habitat use during the spring-summer was studied through analysis of the data derived from the trapping and radio-tracking studies. At the population scale, habitat selection was defined as the general habitat type (such as woodland, pasture, hedge, arable) used by the toad, where preference was indicated by adult density derived from the trapping studies. The circular HSEs in the Rookery, Spinney and the drift fence enclosing the Wood were closed (i.e. made toad-proof) in autumn of 1991 and 1992, so that the following spring catch indicated the summer density in each of the habitats. Density was calculated simply as the number of toads caught in each HSE and represented as toads/hectare.

For the individual, patterns of habitat use were derived from the radio-tracking studies. Two forms of analysis were used. Neu *et al.* (1974) presents a method of evaluating habitat preference using an extension of a chi-squared analysis. If a

significant chi-squared value occurs (indicating a lack of homogeneity), the level of observed use of each habitat is compared with its availability through a Bonferroni *z* statistic. Using this statistic, confidence intervals are built around the observed use of each available habitat. If the chi-squared value calculated for the habitat is below the lower confidence limit, then that habitat was used at the level lower than its availability would suggest (avoidance) and if the value is above the higher confidence limit then the habitat was used over its availability (preference), Table 3.2.

Aebischer, Robertson and Kenward (1993) question the use of preference/avoidance tests based upon chi-squared analysis, since the 'avoidance' of one habitat type will almost invariably lead to apparent preference for another. In addition, analyses that take the radio-location as the sample unit and the number of fixes, usually pooled over several individuals, as the sample size, can lead to two separate forms of non-independence. First, the location of consecutive fixes from a tagged individual are likely to be correlated (Swihart and Slade 1985). Second, pooling data over several individuals is only justifiable if they do not differ in behaviour. Both these problems will inflate the number of degrees of freedom and render the statistical tests over-sensitive (Aebischer, Robertson and Kenward 1993).

To avoid these problems, compositional analysis (Aitchinson 1986) may be applied, where all habitat types are considered simultaneously and data independence is achieved by considering the *animal* as the sampling unit rather than the radio-fixes (Aebischer and Robertson 1992, Aebischer, Robertson and Kenward 1993). The combined proportions of total and utilised habitat are considered equal to 1. They are rendered independent and normally distributed by logratio transformation $\ln(p/q)$, where $q = 1- p$.

The use of the available habitats is regarded in two levels. First the whole of the defined study area, and second that area within the defined study area delimited by the animal's movements, normally a home range defined by the Minimum Convex Polygon (MCP). To examine the selection at the first level, the proportion of each

TABLE 3.2: Occurrence of radio-fixes for target animal based on an initial chi-squared test to determine hypothesis of random selection.

Habitat	Total area (m^2)	Pi	Observed	Expected	Po	Interval
A	165	0.198	107	24	0.863	0.761-0.935
B	205	0.246	13	30	0.131	0.041-0.169
C	207	0.248	2	31	0.016	0.000-0.043
D	222	0.267	1	33	0.008	0.000-0.026

Where Pi represents the proportion of the total area
Po represents the proportion of the radio-fixes observed in each habitat

Expected frequency represents the number of radio-fixes occurring if utilisation is in exact proportion to habitat availability.

The confidence interval represent the theoretical proportion of occurrence and is compared with the corresponding Pi to determine the hypothesis of proportional use. If Po > than the interval the habitat is used over and above that which could be expected given availability, if Po < than the interval the habitat is under-used.

(after Neu *et al.* 1974)

available habitat within the MCP is compared with its availability within the whole study area. At the second level, the habitat composition within each MCP home range is considered the full extent of available habitat and this is compared to habitat utilisation as described by the distribution of the radio locations with the home range (Aebischer and Robertson 1992). Where comparison of habitat use produces a negative value, the habitat used as the numerator in the logratio equation is used more often than the habitat used as the denominator (in proportion to availability). For example, in Table 3.3, the proportion of open-canopy woodland with ground cover was used as the denominator in the logratio transformation of the other 7 habitats (from Aebischer and Robertson 1992). Once each habitat is compared to all the others (by changing the denominator) a matrix is created showing comparative habitat utilisation, Table 3.4.

The location radio-fixes were used to calculate home range size using the Ranges V animal location software (Kenward 1990). Home range size was calculated for the toads released in the test-enclosure, although these data should be viewed with caution since the animals were restricted within the enclosure. At Little Wittenham home ranges where estimated using Loman (1994), where the home range size was calculated based upon a circle encompassing 95% of the recorded catches.

The number of toads observed on each evening was used as an indication of collective activity, both during the breeding migration (but see definitions in Chapter 6) and during the summer period.

Individual activity patterns, derived from the radio-tracking were quantified as the mean distance moved (m/evening) and as the maximum observed movement (Tew 1992). Activity was expressed by the number of evenings where movement occurred as a fraction of the total number of evenings over which the toads were tracked.

3.13 Weather data

Weather data (maximum and minimum air temperature, pressure, wind speed, sunshine hours, precipitation) were obtained from the East Midlands Airport,

TABLE 3.3: Percentage habitat composition within the minimum convex polygon (MCP) home-range estimate of radio-tagged pheasant number 246, and within the total study area. The calculation of the difference between logratios is demonstrated, using the second column as denominator, for an evaluation of habitat utilisation.

	Edge				Non-edge			
Canopy	**None**	**Open**	**Closed**	**Closed**	**None**	**Open**	**Closed**	**Closed**
Ground cover	Yes	Yes	Yes	No	Yes	Yes	Yes	No
MCP area	7.4	5.9	22.5	0.1	0.1	49.3	8.5	7.8
Total area	21.6	3.6	9.3	10.4	16.9	11.6	9.1	13.4
Logratios (MCP)	0.227		1.339	-4.078	-4.078	2.123	0.365	0.279
Logratio (Total)	1.792		0.949	1.061	1.546	1.170	0.927	1.314
Difference	-1.565		0.390	-5.139	-5.624	0.953	-0.562	-1.035

TABLE 3.4: Matrix of logratio differences between utilized (MCP home range) and available (total study area) habitat composition for radio-tracked pheasant number 246. The implications for habitat are noted by sum the number of positive and negative signs in each row. The habitat with the highest number of positive logratios is the favoured habitat.

			Edge				Non-edge			
	Canopy		None	Open	Closed	Closed	None	Open	Closed	Closed
		Cover	Yes	Yes	Yes	No	Yes	Yes	Yes	No
Edge	None	Yes		-1.565	-1.955	3.573	4.059	-2.518	-1.003	-0.503
	Open	Yes	1.565		-0.390	5.139	5.624	-0.953	0.562	1.035
	Closed	Yes	1.955	0.390		5.528	6.013	-0.563	0.951	1.424
	Closed	No	-3.573	-5.139	-5.528		0.486	-6.092	-4.577	-4.104
Non-	None	Yes	-4.059	-5.624	-6.013	-0.486		-6.577	-5.062	-4.589
edge	Open	Yes	2.518	0.953	0.563	6.092	6.577		1.515	-1.988
	Closed	Yes	1.003	-0.562	-0.951	4.577	5.062	-1.515		0.0473
	Closed	No	0.530	-1.035	-1.424	4.104	4.589	1.988	-0.473	

(From Aebischer and Robertson, 1992)

located 20 miles from Osbaston and reported in the local paper (Leicester Mercury). During the breeding season at Osbaston weather data were also collected by hand and at Coleorton hygrometers and thermometers were placed in all four habitats during the summer. At Little Wittenham the weather data (maximum and minimum air temperature, pressure, wind speed, precipitation) were obtained from a station around 1km away from the ponds.

3.14 Statistical Analyses

Statistical analyses were under taken using the Minitab package at the computer laboratories of De Montfort University. A selection of analyses were used including analysis of variance (ANOVA) for multiple comparison; where the result was significant the Tukey test for unplanned multiple comparisons was used. For single comparisons the Mann-Witney test was applied. Simple linear regression has been applied and where appropriate multiple-regression. Where correlations are used, 'rs' represents the Spearman ranked correlation and 'r' represents the production moment correlation.

Throughout the reporting of the current study where the plus/minus ('±') sign is used to describe the mean this represents the standard error of mean, unless otherwise stated.

Chapter Four: The application of methodologies for remote monitoring and tracking of amphibians

4.1 Introduction

It is not the purpose of this chapter to question the objectives in the cited studies, but consider the application of methodologies used for habitat selection and utilisation studies in amphibians. Telemetry and radio-tracking in ecological studies has developed since the early 1960s and although widely applied in the study of small mammals and birds (see Pride and Swift 1992), its use in herpetology remains limited. Of the 85 papers presented at the European Conference on Wildlife Telemetry in 1991 (Priede and Swift 1992), 68 were based on practical radio-tracking studies, of these, 34 studied mammals (50%), 19 fish (28%), 10 birds (7%) and only 4 papers (6%) specialised in amphibians or reptiles.

4.2 What are the alternatives to radio-tracking ?

4.2.1 Trapping and searches by hand

Trapping and catches by hand during the major activity periods are the most common methods for gaining information on the movements of amphibians (Gittins *et al.* 1980, Gittins 1983c, Oldham and Swan 1991, see Chapter 3). While the data obtained from these studies are resource-effective, in terms of the number of animals that can be caught and processed, they can only be applied to distinct seasonal periods when the species are highly active *en masse*. During migration periods animals may be caught by searching roads and tracks close (usually within 500 metres) to a breeding site. At the peak of breeding activity removal of animals from the water may provide the easiest opportunity to collect a large sample of animals.

The basic assumption made in trapping studies, that the animal shows a preference for the habitat where it was caught, may be incorrect and factors such as trap-baits, trap-addiction and trap odours that occur commonly in small mammal studies (Montgomery 1979, Boonstra, Rod and Carleton 1982, Stoddart and Smith 1986) may have an effect. There is some evidence to support trap bias in amphibia, where upon reaching a drift fence some toads turn back and are not caught (Oldham, Latham and

Arntzen in prep). During breeding, males may be attracted to traps by the release calls of males in the pitfall traps.

Outside of the main migratory periods animals may be located by walking slowly through terrestrial habitat during suitable evenings with a powerful torch and/or by searching potential day-time refugia or creating artificial refugia (Denton and Beebee 1992). Denton and Beebee (1992) evaluated the methods for studying natterjack and common toads outside the breeding season and concluded that night searches were the most successful method. It was estimated that around 10% of a natterjack population could be observed during evening searches by torch light, when climatic conditions were suitable. Common toads, however, prefer to forage in denser vegetation than natterjacks (Mathias 1971, Denton 1991), making observation, therefore more difficult, and it is unlikely that a similar percentage could therefore be achieved even during ideal conditions.

Home-ranges may be constructed using a combination of hand searching and pitfall trapping outside the breeding season. However, for amphibians it may prove difficult to collect sufficient catch locations to build an accurate range, and the process may also involve much disturbance to habitat. Despite this, studies have been completed during the terrestrial phase on home-ranges for anurans using only trapping and hand collection (Haapanen 1970, 1974, Loman 1994).

4.2.2 Radio-active tagging

Breckenridge and Tester (1961) used radio-active tantalum (Ta^{182}) wire placed beneath the surface of the outer skin. Animals could be located in their burrows and in the surrounding habitat to a range of 6-8 metres (Oldham pers. comm.), however the method did not permit toads be individually identified using the radio-active material alone. More recent studies (Heyer *et al.* 1994) have used cobalt-60 tags, providing a detection range of 5m for tracking periods of up to 67 weeks. Studies in North America have tracked species of frogs and salamanders over distances of 2000m. The cost of radio-active tags (£75 each, 1994 prices quoted in Heyer *et al.* 1994) is comparable with radio-transmitters (Biotrack S1-tags, 1994 prices, Cresswell pers. comm.) and tag size (2.0 x 0.3mm) makes it applicable to small individuals, however

there is not the benefit of individual identification or long signal range as for radiotracking.

4.2.3 Trailing devices

Trailing devices have been used to follow the short range movements of the leopard frog *(Rana pipiens*) during summer (Dole 1965) and during both the breeding and summer periods (Sinsch 1987, 1988a, 1998b, 1988c). These devices consisted of a cotton bobbin reel, loaded with thread, and attached to the back of the animal. The thread is released as the animal moves, and the route is marked.

Dole (1965) studied the movement of 136 adult leopard frogs for up to 35 days. He found that movements within the frog's home range were rather infrequent and consisted of short movements centred around a core position, which the frog often returned to. The movements occurred during dusk and continued until day break. Sinsch (1987, 1988a, 1988c) developed the method to study the orientation behaviour of common toads displaced from their breeding site migrational patterns and throughout the activity period of the toad (1988b).

Despite the advantages of the low cost and technical input of this method large scale movements are restricted, since the 'range' of the device is limited to the length of the cotton thread, about 50m (Dole 1965 and Sinsch pers. comm.). Given the sedentary nature of the common toad during its terrestrial period this may not be too much of a hinderance, however toads are known to move distances greater than 50m during a single evening and thus it will be impossible to follow these movements. The addition of a relatively large object on the back of an animal may increase its predation risk and may also prevent it from using certain refugia. The technique is also probably limited to individuals over 60mm DLU, with the bobbin reel weighing about 8.5g.

4.2.4 Passive transponders and PIT tags

Passive transponders (suppliers RS Biotech, Finedon, Northants, England) are used widely in biomedical sciences as a form of unique marking in laboratory animals (Forbes pers. comm.). Each tag is pre-programmed with a unique 8-digit alphanumeric code, which is read by a hand-held scanner. The scanner produces a magnetic field

which activates the transponder and echoes the coding. Since there is no internal power source, the tags have an unlimited life span. Sinsch (1992a) provides a review of this technique for use in the field with juvenile natterjack toads where the scanner was fixed to a handle and swept across the ground in a systemic fashion (supplied by FishEagle Co., Lechlade, Gloucestershire) in an attempt to locate the individuals. Other researchers have used transponders for newts (Fasola, Barbieri and Canova 1993), the common frog (Brown pers. comm.) and reptiles (Camper and Dixon 1988) as an alternative to toe-clipping for tagging and identification, recording little impact in terms of loss in mass or increase in mortality.

The major advantages of these tags over radio transmitters are their cost (£5 compared to £61, 1994 prices), the cost of scanner is, however, £700 compared to £400 for the M-57 Mariner receiver (1994 prices, Mariner Radar, Lowestoft, Suffolk, U.K.) and size (1.8mm x 12mm, mass 100mg), against radio-transmitters (16mm x 9mm x 6mm, 2500mg). The smaller size of the PIT tag permits tracking of animals as small as 30mm snout-vent length (Sinsch 1992), or 2g (Fasola *et al.* 1993) that could not be tagged using radio-transmitters. The method appears attractive for studying survival of individuals after the juvenile stage and can be used to identify animals once recaptured. The transponders can be read by a hand scanner and recorded directly into computer and stored on a data base. The tags, however, have only a short response range (less than 10cm) which makes them more difficult to apply to habitat utilisation studies, despite Sinsch (1992a). The cost may also become an issue given the large number of tags required given the predicted tag loss through mortality during the juvenile stage.

Passive transponders offer a possible application for tracking small individuals, but their short response range and lack of application for tracking animals over distances greater than 5m, means they, perhaps, are only really an alternative to toe-clipping.

4.2.5 Binary coded micro-tags

Injection of micro-tags (binary coded wire) beneath a toad's outer layer of skin, permits tracking of the toad through the use of a metal detector (Sinsch 1992a). Coded wire allows identification of the individual, but only after removal of the micro-tag and the

response range is similar to that of the transponders. Fuse-wire, or another inert metal, could replace the need for binary coded wire reducing the cost, whilst still permitting tracking, but losing identification (unless animals are toe-clipped or Panjet marked). The benefit of this technique is the relative cost and ease of access to the equipment, and the lack of need for specialist knowledge.

4.3 The application of radio-tracking to amphibian research

4.3.1 Introduction

The earliest published work applying radio-tracking techniques to amphibia was completed by Tester (1963)[1] studying the American toad, *Bufo americanus*. The study used a relatively large tag (c. 7.0g) that was attached to the toad using a back-harness. More recent studies on other anuran species using radio transmitters have included migratory and reproductive behaviour (van Gelder *et al.* 1986a, Sinsch 1988, 1992b), body temperature during hibernation (van Gelder *et al.* 1986b), thermoregulation at high altitudes (Pearson and Bradford 1976), hibernacula selection (Bosman, van Gelder and Strijbosch H. 1996) and comparative habitat ecology (Denton 1991), in addition to technical studies (Nuland and Claus 1983), Table 4.1.

The growth in the application of radio-tracking in amphibian research has stemmed from the increased availability of miniature transmitters (UK suppliers Biotrack, Stoborough, Wareham, Dorest also Holohil Systems Ltd, 3387 Stonecrest Road, Woodlawn, Ontario, Canada). Despite the advantages of the alternatives to radio-tracking, mainly cost and low technical input, no single method can provide the ability to monitoring the movements of a known individual with limited disturbance to its normal pattern of activity as that achieved with radio-tracking. It is for this reason that radio-tracking has been the preferred technique for ecological studies of a number of species (see Priede and Swift 1992). There remain some difficulties that need to be considered in the application of radio-tracking in any ecological study and these have been highlighted in the following sections with special reference to herptiles.

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[1] The original manuscript for this reference could not be located and the details are cited from Nuland and Claus (1983).

Table 4.1 Review of the application radio-tracking in amphibian studies.

1 Force-feeding of radio-tag to the target species
2 Surgical implantation of the tag into the body cavity of the target species
3 External attachment of transmitter via body harness
4 Not known

Author	Species studied	Attachment	Dimensions	Load ratio (%)	Range (m)	Life (days)
Tester (1963)	*Bufo americanus*	Back-harness[3]	7.0 g	NK[4]	NK	10 - 30
Pearson and Bradford (1976)	*Bufo spinulosus*	Ingestion[1]	7x17 mm	NK	NK	NK
Nuland,van and Claus (1981)	*Bufo bufo*	Back-harness[3]	10x10x3mm 3.0 g	6- 13	50 - 100m	95 - 150
Stouffer et al. (1983)	*Cryptobranchus alleganiensis* (5)	implantation[2]	48x16mm 11.6g	NK	100m	150 - 180
Olders et al. (1985)	*Bufo bufo*	Implantation[2]	3.0g	8 - 11	40m	180
Fukuyama et al. (1988)	*Buergeria buergeria* (6)	Back-harness[3]	0.9g	6 - 7	10m	8
Sinsch (1988)	*Bufo calamita* (6: 5 males, 1 female)	Implantation[2]	2.5g	NK	40 - 200 m	90
Denton (1991)	*Bufo calamita* (40) *Bufo bufo* (4)	Implantation[2]	2.0 -2.8g	5 - 7	200 m	30 - 100
Seitz et al. (1992)	*Rana temporaria* (28)	Implantation[2]	3.5 - 3.6g	7 - 13	100 m	33 - 50
Swan & Oldham (1992)	*Bufo bufo* (40) *Rana temporia* (14)	Ingestion[1]	2.5g	5 - 10	150 m	30-60

4.3.2 Reception range and tag life-span

Reception range and tag life-span are linked to the available power source within the radio-tag. Increasing the available power provides a greater range and signal life-span, but necessitates an increase in the mass of the tag. The power source in most tags can make up to 60-70% of the total tag weight (Kenward 1989), therefore a decision has to be made either to accept a heavier tag with a longer life-span, or a lighter tag with a shorter life-span.

A loading ratio (the mass of the tag compared to the mass of the target species) of 5-10% of animal body weight has been suggested (Kenward 1989), above this figure the tag is believed to be a burden on the normal activities of the target species. One adaptation developed for tracking small animals is a pulsed signal. This reduces the energy demand since the tag is not continuously transmitting and effectively increases tag's life-span.

The reported reception range in previous amphibian research has varied between 40-200 metres, Table 4.1. Adult toads can cover distances of over 250m during an evening and the relatively short reception ranges can lead to the 'loss' of animals without intensive study during tracking. The reception range can be influenced by a number of factors apart from the power source. Dense vegetation has the effect of dampening the signal power and causes 'signal bounce' (Hupp and Ratti 1983). The orientation of the tag in relation to the axis of the receiving antenna influences signal reception patterns (see Chapter 5). In addition, the signal range reduces as the tag is depleted of power; the decline is more rapid once the tag has reached around 75% of its life span (Creswell pers. comm.). Although, tags are still functional beyond this period, the signal is noticeably weaker. All these features may affect the accuracy of location estimates.

Tracking studies that use VHF radio-transmitters can lose accuracy when estimating bearings due to signal reflection and absorption (Pride 1992). Using triangulation to determine the location estimates can compound these errors since a relatively small error in the bearing estimate can lead large discrepancies between the actual and estimated location (Springer 1979).

The reported life-span for the tags used in the studies reviewed in Table 4.1 provides tracking periods of less than 100 days. Although the number of effective days may be lower, given the reduction in reception range as the tag's cell is depleted. Experience gained during the current study suggests that a realistic life-span for a small single cell tag was c. 60 days. This reduces the opportunities for the application of radio-tracking, even using the upper limit of 100 days, tracking may not be able to be continued during the over-wintering period (October/November-February/March) without the need to change the tag.

4.3.3 Experimental design and statistical considerations

The time and resources required to locate animals using radio-telemetry usually results in studies relying on data derived from only a limited number of individuals. To compensate for small sample size, some studies have used large data sets from these single animals (Sinsch 1988c). Increasing the time period of study for a small number of target individuals to increase available data is statistically inappropriate, since the animal itself, rather than the radio-location, should be considered as the sampling unit. Limited data over a number of tracked animals is statistically more valid than extensive data based on a single animal (Aebischer and Robertson 1992). Projects based on a few (<20) animals, intensively tracked cannot adequately measure the between-animal variation that is necessary for conclusions based at the population level.

Data obtained from extensive studies also suffer difficulties in analysis through statistical independence. Large amounts of successive radio fixes are unlikely to be independent since the individual location estimations are a function of the time interval between them (Swihart and Slade 1985). Statistical independence may be achieved through sub-sampling the existing data. Alternatively, the time taken for an animal to cross its home-range may be used as a suitable time period to assume data independence between individual radio-fixes (White and Garrott 1990).

4.3.4 Transmitter attachment

Transmitters have been attached to amphibians externally, through a harness or waist-band or implanted, through surgical implantation or by ingestion (force-feeding), Table 4.1. Each method may have an impact on the animal which may be short-term or

long-term. Short-term effects are related to the period after tag-attachment whereas long-term effects are more permanent causing disabling effects that can influence animal behaviour. Short-term effects include excessive preening and shaking in birds (Greenwood and Sergeant 1973, Gilmer *et al.* 1974) and increased reclusive behaviour in voles (Leuze 1980). These effects occur whilst the animal becomes acclimatised to the tag. Toads have been observed to be more reclusive immediately after surgery (Beebee pers. comm.), which might lead to bias in habitat selection. Short-term effects are unlikely to seriously hamper tracking studies, as long as data from newly tagged animals are viewed with caution.

The long-term effects of tagging are more serious; snakes have suffered post-anaesthesia heart failure (Charland 1991), reduced and impaired movement (Fitch and Shirer 1971) and changes in foraging behaviour (Lutterschmidt and Reinert, 1982). This latter reaction is a particular problem with stomach-ingested tags where foraging behaviour and basking time is related to how full the stomach is. Amphibians have been reported to suffer laceration (Oldham and Swan 1992) or have drowned (Van Gelder et al. 1985) where radio-tags are attached using harnesses.

External attachment of radio-tags to amphibians and reptiles has proved to be erratic in the level of success. The moist nature of amphibian skin precludes direct attachment of transmitters with glue. Harnesses and waistbands have been used, although detachment is commonly reported in dense vegetation and during swimming (van Gelder *et al.* 1985). There have been successful studies, notably Fukyamma *et al.* (1988) where small stream frogs (*Buergeria buergeri*, average female size 14.2g) were fitted with waist bands holding radio-transmitters and followed over eight days, also green toads (*Bufo viridis*) and natterjack toads have been followed through a mixture of habitats with backpacks (Baumgart 1993, Golay 1994). An advantage with an external tag is the possible addition of an external antenna that increases the reception distance, although this may hinder movement and increase predation risk.

The two most widely practised forms of internal tag attachment for amphibians are ingestion or force-feeding and implantation. Ingestion of a relative large object might be considered to influence subsequent feeding behaviour. However, research by

Oldham and Swan (1992) on the common frog and the common toad illustrated that the force-feeding of tags weighing 2-2.5g with dimensions of 16mm x 9mm x 6mm showed no significant impact of appetite (range in animal mass *B. bufo* males 18-53g, females 17-88g, *R. temporaria* 11-47g). Tags were retained in the stomach for a mean of 15 days in the male common toads and 6 days for the common frog. Since both these species are regarded as opportunist feeders and appear to eat even if stomachs are full (Larsen[2] 1984) it seems unlikely that an object held within the stomach would affect eating patterns, as is observed in snakes (Lutterschmidt and Reinert, 1982). The difficulty observed with force-feeding radio-tags is the unpredictability in the length of tag retention, although evidence collected during the current study (Chapter 7) shows a positive correlation between tag retention time and body size. Unless positive identification of the toad occurs at regular intervals during tracking the toad can be lost when the tag is regurgitated and this, in part, has consequences on the level of disturbance at the animal.

Implantation of a radio-tag into the body cavity of an animal requires a surgical operation. Removal of animal from the field situation followed by surgery may cause stress or even mortality. Sinsch (pers. comm.) reported a mortality of only 5%, and Charland (1991) illustrated no difference in the litter size or gestation period for garter snakes following implantation. However, Denton (1991) believed that the fresh wounds increased the chances of predation on natterjack toads by grass snakes. This can be rectified by ensuring the wounds have healed at the time of release. Implantation does not appear to damage the internal organs of anurans; normal egg production, breeding and spawning have been shown to occur in one individual common frog following surgical implantation of a radio-tag (Bosman pers. comm.).

Surgical implantation does ensures than toads are not lost if the tag is regurgitated prematurely, however there have been no published studies on the behaviour of toads following implantation and therefore the impact is uncertain.

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[2] In this study toads were force-feed meal worms and continued to eat the worms even when live worms were passed through the toads cloaca.

In the current study tags were ingested since this offers an easy and quick form of tag attachment, which can be completed in the field without need to remove the toad from the field. Although the method is hindered by a relatively short and variable retention period (c. 30 days) compared with surgical implantation, it was considered preferable on the ground of its convenience. Animals where tracked for periods of up to 30 days, to avoid loss of tag and toad.

Chapter Five: Development of the automated tracking system

5.1 Introduction

Radio waves are electromagnetic waves and therefore subject to interference from external sources through reflection and refraction. There audible range is subject to distance decay, which follows the inverse-square law, i.e. the strength of signal is reduced by 75% if the range is doubled (French pers. comm.).

The three-element Yagi antenna used in both the automated system and the Mariner 57 hand-receiver has a characteristic reception pattern with well-defined peak and null locations. The strongest peak occurs when the shortest element of the Yagi is in line with source of the received signa with smaller peaks occur to the sides.

Radio-tracking individual animals by hand is a time consuming process. Target species that are either nocturnal or crepuscular, such as amphibians, rodents, bats are reclusive and tracking can result in the disturbance of normal activities and damage to refugia, leaving an animal vulnerable to predation or desiccation (Denton pers. comm.). This will have an impact on the validity of the results. Some researchers claim that animals eventually became accustomed to the presence of the fieldworkers (Tew pers. comm.) this itself may lead to biased results. The simplest form of location estimation involves following the source of the signal until its amplitude reaches a peak and/or the animal is observed allowing identification, then marking its location. Triangulation uses bearings obtained from two or more receivers at known locations, remote from the transmitter's location. The animal's location is obtained by the intercept of the bearings obtained from the receiver. Accurate triangulation requires knowledge of the location of the radio-tracker and the bearing angle, this may be difficult if the tracker is continually on the move.

Whilst hand-tracking can be a laborious task, the advantage of the development of an automated system is the ability to continually follow the movements of the target species in a remote manner. Since location estimates can be generated without the need of disturbing the animal, then the problems of disrupting normal activities are reduced. Automated tracking is more efficient in terms of data collection, since a large

number of animals may be followed at once. Bearings are calculated from fixed location, making triangulation less prone to operator error during tracking exercises. The automated system developed at Coleorton used simple triangulation from two fixed point antennae, using the loudest signal method (Springer 1979).

5.2 System description

5.2.1 Hardware and equipment

The hardware associated with the automated tracking system was designed by Dr. John French of Mariner Radar, Lowestoft, Suffolk, UK. The design allowed both manual operation and control through an automated system. The automated system was designed to be easily constructed, robust, and flexible. The software was designed by the author of the current study. The system comprised an IBM AT computer with monochrome graphics and hard drive for data storage and Analog/Digital Input/Output card, VHF receiver with R232 control of frequency, a receiver to antenna interface and a receiver to computer interface with two Yagi three-element antennae mounted on rotator units (see French, Latham, Oldham and Bullock 1992).

5.2.2 Location of system

The system was installed in an enclosure constructed in a semi-walled garden at Coleorton, North-West Leicestershire. This site was 500m from a large toad population that had been studied since 1982 (Oldham 1985, Oldham and Swan 1991). The enclosure was established as part of the JAEP study and constructed during 1990, with a total area of 846 m^2, measuring c. 30m by 45m (Smithson 1991). The enclosure was maintained during 1990-1992 under distinct habitats and surrounded by a toad-proof fence. These four habitats were, an open cultivated area (A), a low cut amenity lawn (B), a rank tall herb and grassland (C) and a section of woodland scrub (D). A box hedge divided the cultivated section and the amenity grassland, forming a fifth edge habitat (E).

During the winter of 1992 the garden site and surrounding fields were surveyed with help from Mr. R. Ashton of the Department of Building at De Montfort University and

plotted using the University Computer Aided Design System, Figure 5.1.

5.2.3 Radio transmitters and frequencies

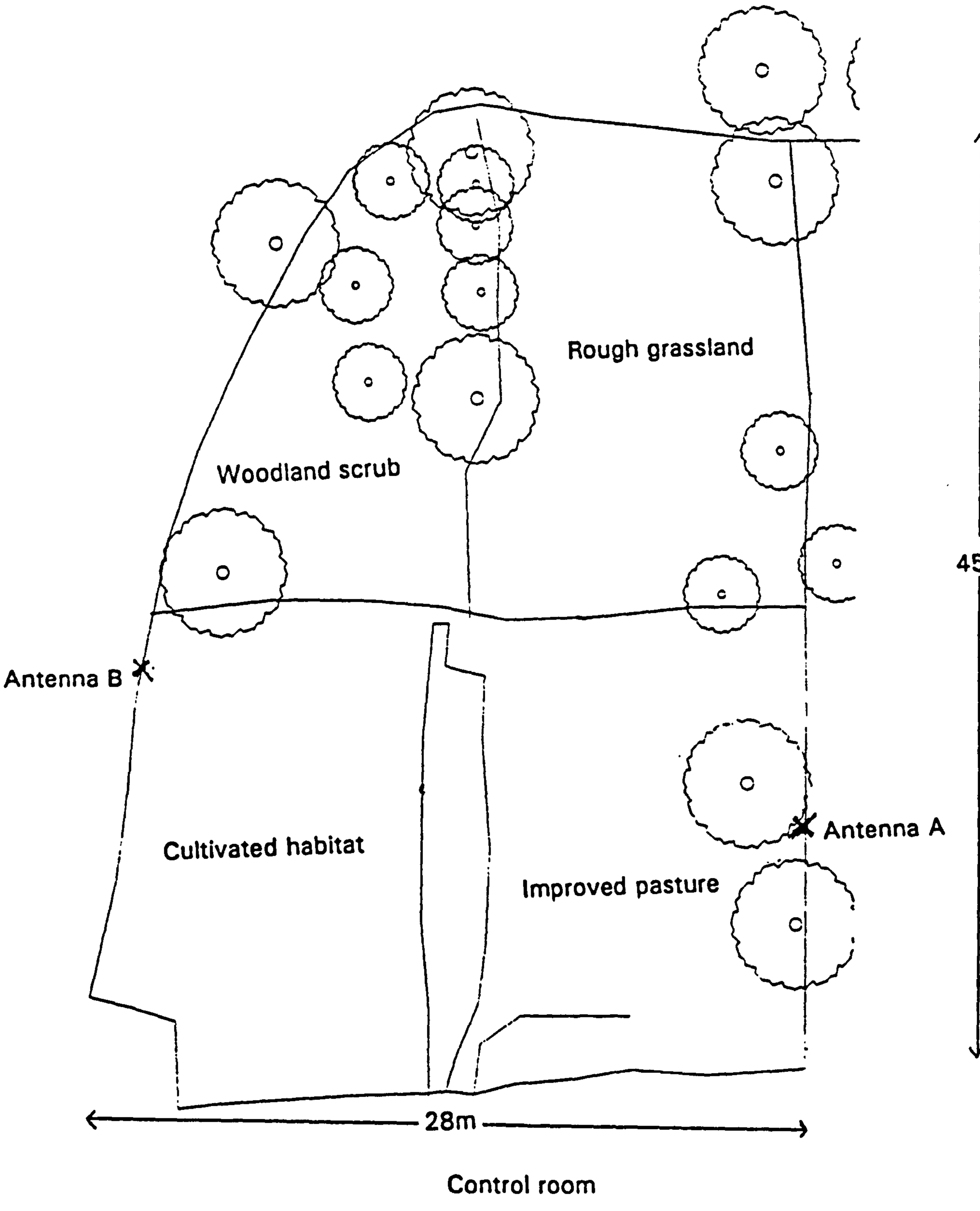
The automated system was designed to function with VHF Biotrack S1 transmitters, used extensively with woodmice (Wilson *et al.* 1992, Tew 1992), bats (Jones and Morton 1992), moles (Gorman *et al.* 1992) and both the natterjack and common toad (Denton 1991, Swan and Oldham 1992, French *et al.* 1992). The complete tag weighs between 2 and 2.5g, with the dimensions of 16 x 9 x 6mm. This represents some 6-7% of a toad's mass, within the accepted 5-10% load increase (Kenward 1989). The transmitters use a single transistor to produce a pulsed signal that has a distinctive signal pattern with polarisation mainly horizontal. Pulsing the signal reduces the energy use and increases tag life span. The legal band ranges for radio-tracking in the U. K. are 104.6-105.0MHz and 173.20-173.35MHz (Kenward 1989). The upper band was used for the current study.

Each tag was tuned to an individual frequency so that simultaneous tracking of a number of individuals was possible. A minimum 5KHz was selected between tags that were used simultaneously. Tags that had frequencies within 5KHz of one another overlapped and resulted in some difficulty in determining true lines of peak signal amplitude.

5.2.4 Location and operation of the antennae

The system contained two three-element Yagi antennae mounted on rotational units. The units were connected to the computer system by 50m low loss cables. White (1985) presents results based on a series of computer simulations to determine the optimal locations of fixed antenna towers. He concludes for two-tower systems, the towers should be located off the study site so that the antenna baseline did not cross the site. At Coleorton, location of the antennae at the end of the enclosure close to the control centre would satisfy White (1985), but would be undesirable since it maximized the distance between the antennae and the woodland area, see Figure 5.1. Location accuracy was likely to be hampered by high reflection and signal absorption in the woodland (Hupp and Ratti 1983), and a weaker signal due to known distance decay was also undesirable. Location of the antennae at the opposite end of the

Figure 5.1: Radio-tracking enclosure, Coleorton. As CAD surveyed during the winter of 1991 and produced by R. Ashton.



study enclosure would also satisfy the requirements of White (1985), but would require cables of over 75m, requiring additional current boosters to compensate for the current loss through resistance.

The compromise was to reduce the distance to all site extremities to a minimum, so keeping the signal to noise ratio as high as possible and the antennae were located as indicated. However should an location estimation lie on the baseline, animals could not be located. To remove this problem, when a location was estimated along the baseline a clause in the software compared the signal strength received at the two antennae and used this ratio to assess the location of the animal along the baseline. However, the intercept angle remains very narrow, and therefore location estimates were vulnerable to inaccuracy.

During the initial installation of the tracking system the antennae were moved to the hard left position shown on the controllers, and the Yagi elements were then placed in line with the defined grid pattern, parallel to one another, but facing opposite directions, and secured. Both antennae rotated in a clockwise direction. During manual and automatic operation the signal strength was measured through a range of angles for each of the two antennae. When the system was operated manually the antennae were rotated using the switches on the controllers and the maximum signal strength decided by the operator using the loudest signal (Springer 1979). From the angles indicated on the meters on the control boxes, the point of intersect was calculated using simple trigonometry. During automated operation the peak and null locations were identified by a digital processing technique detailed below.

5.3 Design of the controlling software

Software was written in Microsoft Quickbasic 4.5. The function of the programme can be divided into three main categories, the control of the antennae, the filter and processing of the data and location estimation.

5.3.1 Control of the antennae

At a set time (during the current study defined as an hour before sunset) the receiver was tuned with a resolution of 100Hz to the frequency of the first toad to be located.

The interface connected antenna A to the receiver and a sample of 2000 readings collected, filtered, processed and stored with the angle code and a weighting value (represented by the number of pulse peaks identified by the filtering processes). Antenna A was then moved 10° from the start position and a second data set collected. This process was repeated until antenna A completed a full sweep of the study area, about 120°. The interface then selected antenna B and the process repeated as for A..

5.3.2 Signal filtering, processing and recognition

The S1 tag produced the signal pattern shown in Figure 5.2a. The system used stomach ingested tags with no external antenna, thus the signal to noise ratio was never very high and the signal data package showed high interference. Digital signal processing, based on the signal characteristics of pulse rate and duration was developed to remove interference.

Initially, the mean value of the unprocessed data set of sample signal strengths (n = 2000) was calculated. Each sample point within the unprocessed data set was then compared to the mean. It was assumed that since the signal from the tag was recorded in addition to the background noise; this would always be greater than the mean, thus those values less that the mean represented noise alone and were rejected. Points that were rejected were given a value of 0, while accepted values were set to 1, Figure 5.2b. Using the mean as a threshold permitted the filter to re-calibrate itself with each new set of data. The median would have been more appropriate as a representative of the overall background noise level, however this increased processing time to an impractical length, especially given the required duplication of this process during operation.

Impulses caused by engine ignition systems, central locking systems, electronic alarm systems and to a limited extent atmospheric static produced signal pulses similar to the tag's were not rejected by this initial processing. These rogue impulses would decrease the efficiency of location estimation, especially when dealing with a weak signal. Pulse duration was used as a second form of filtering; any pulse that did not match the S1 tag characteristics was eliminated. The pulsed signal of the S1 tag had

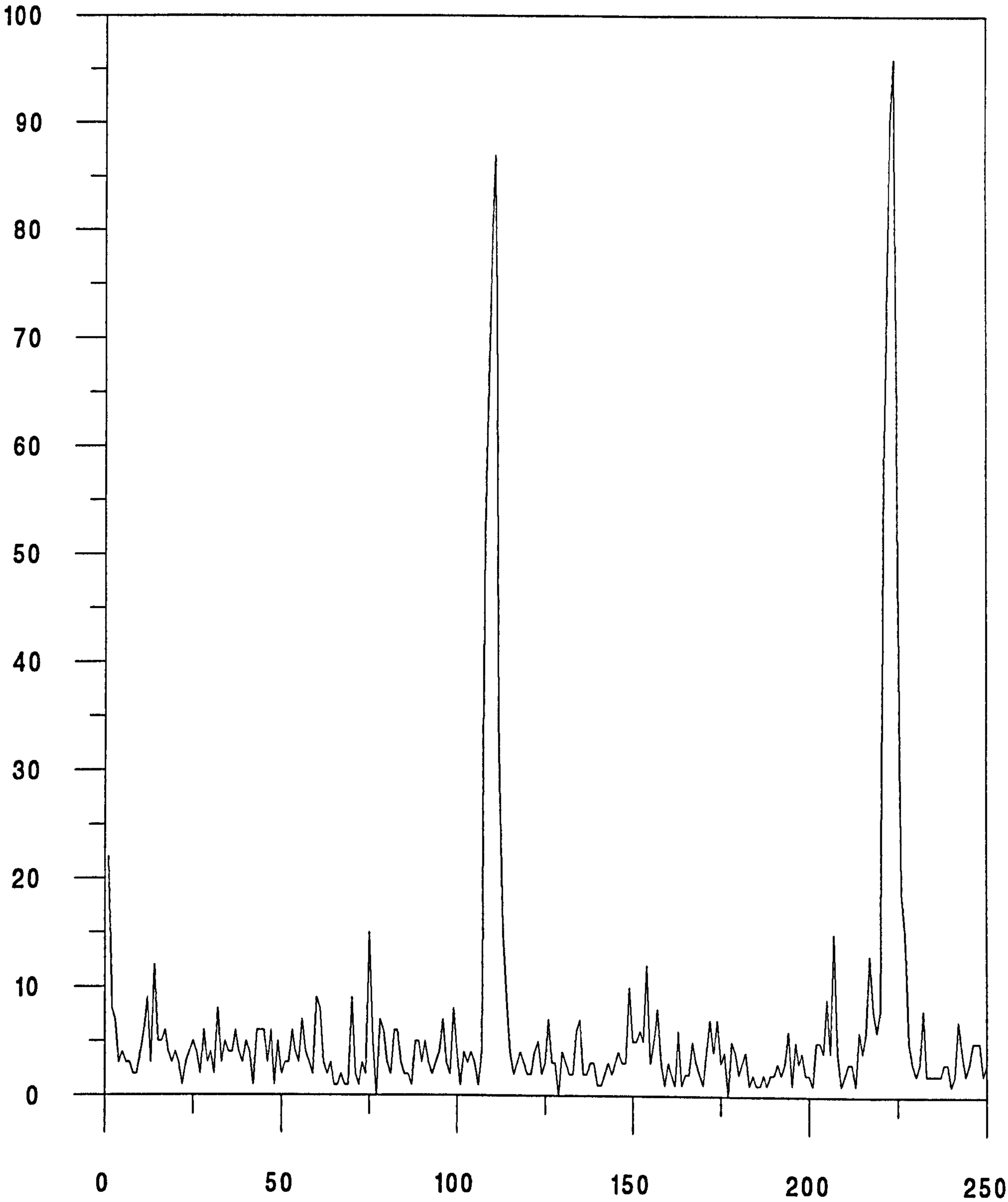


Figure 5.2a: Typical signal amplitude from a strong signal, before filtering. The peaks, representing the pulses from the S1 tag, can be easily seen against the background noise.

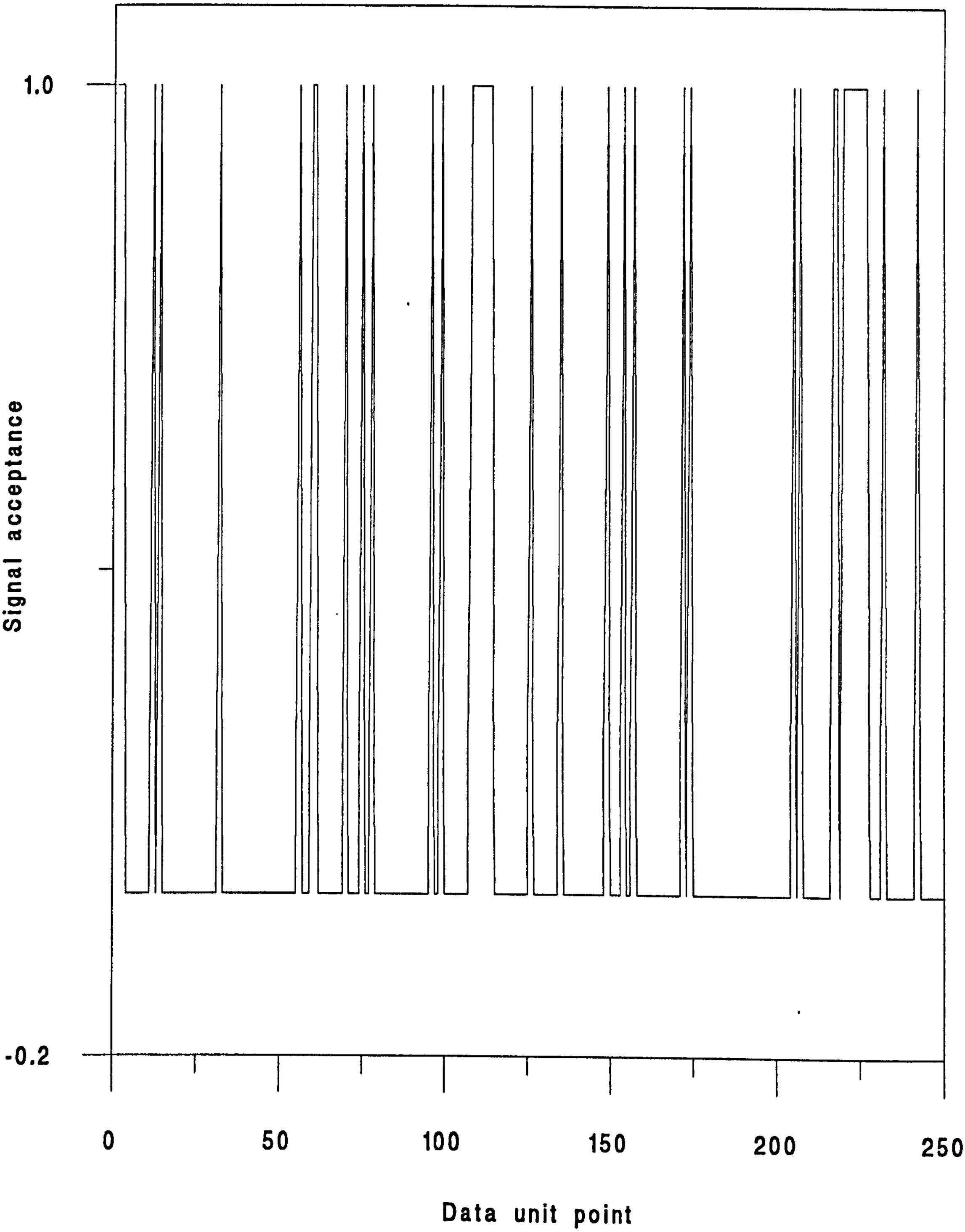


Figure 5.2b: First stage of filtering, where all low level background noise is removed. The acceptance level is either 1 or 0.

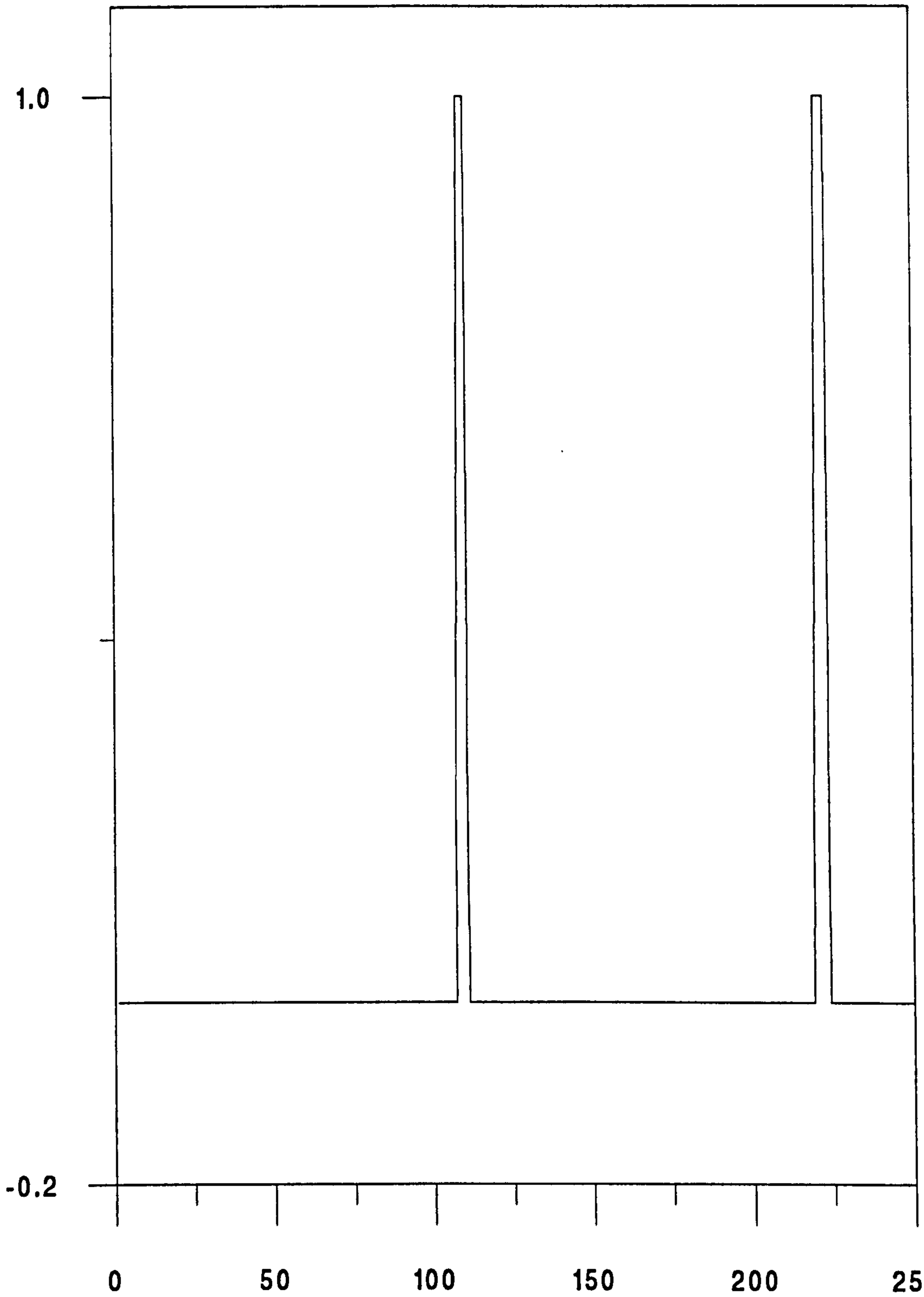


Figure 5.2c: Second stage of filtering; where peaks that do not match the specified time period are removed. All noise has now been removed and the signal has been correctly identified (see Figure 5.2a).

a defined length. The filter consisted of a moving five-point average and this was applied to the newly processed data set (where each value was either 1 or 0). Where the sum of the five-point average was equal to 1, a peak of 5 or more individual sample points had been recognised with a value greater than the mean and a pulse had been identified. The value for this data point was assigned to 1. Where the average was less than 1, no pulse was present or lasted for a shorter period than the acceptance threshold. This was classified as 0. The final data set consisted of a series of 0 values that were inter-spaced by three or four 1 values, Figure 5.2c.

Given a powerful signal from the tag the pulses were easily recognised and processing was simple. However, if the tag was located at a distance over 50m, battery level was low, or the noise to signal ratio was low, the pulse peaks were less easy to identify making the processing less successful (Figures 5.3a to 5.3c).

The full filtering process is illustrated in the flow diagram, Figure 5.4.

5.3.3 Location estimation

Once both antennae had completed their rotations, the processed data set consisted of a series of readings; the signal strength, angle and number of recognised peaks at 10° intervals, Figure 5.5a. These data were used to produce a polynomial curve fit representing the estimating signal strength at 1° intervals, Figure 5.5b. The maximum amplitude of this curve was calculated and the associated angle represented for each antenna was assigned for tag location. Given the known locations of the two antennae and the geometry of the site, the location of the toad was estimated using trigonometry.

After final location estimation, the antennae were then returned to their rest positions, the receiver tuned to the next frequency and the process was repeated. The full process took six to eight minutes, the majority of the time was taken for the low grade 286 computer to complete the processing.

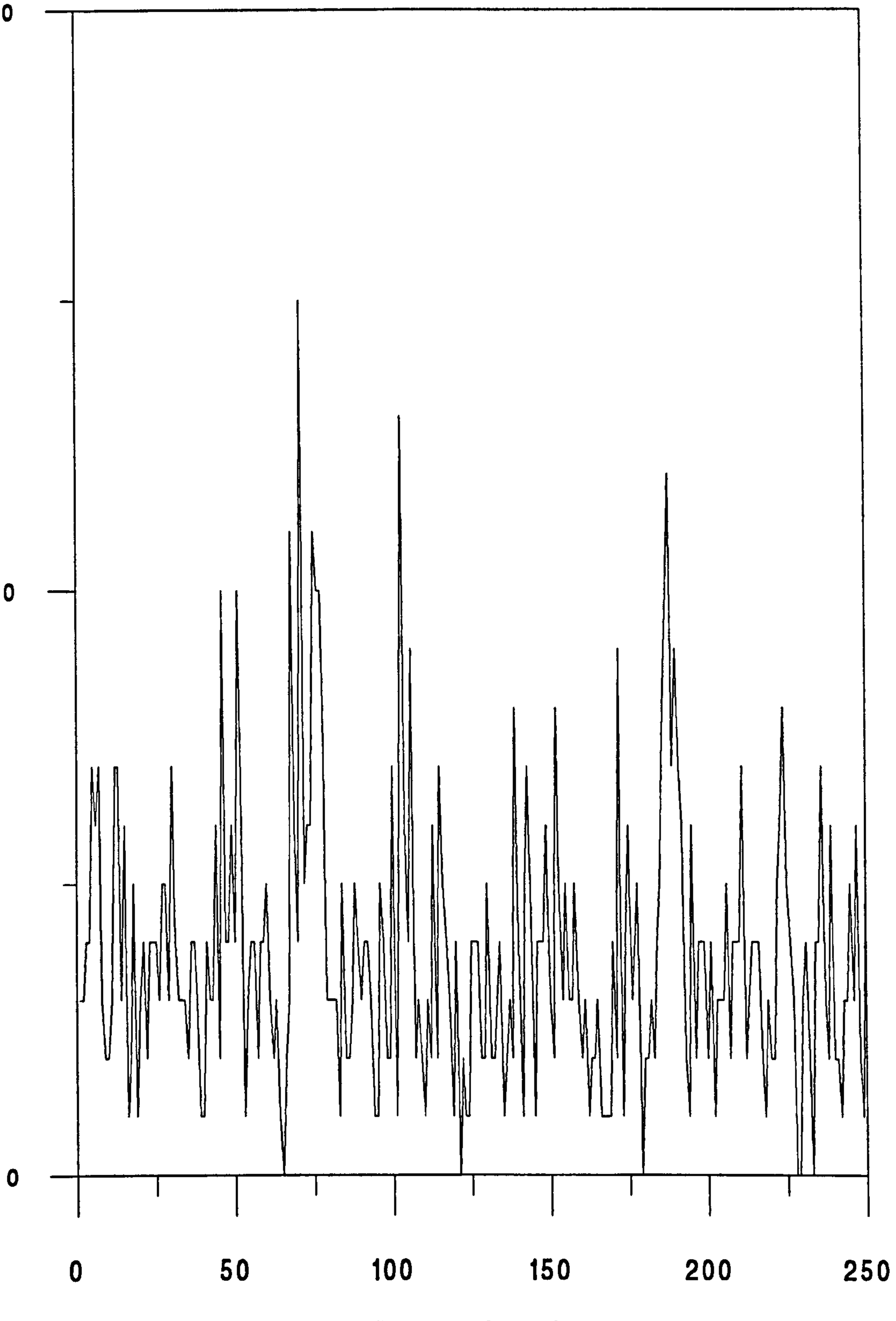


Figure 5.3a: Typical amplitude from a weak signal. When the signal:noise ratio is low the peaks representing the actual pulses are very difficult to recognise against the background noise.

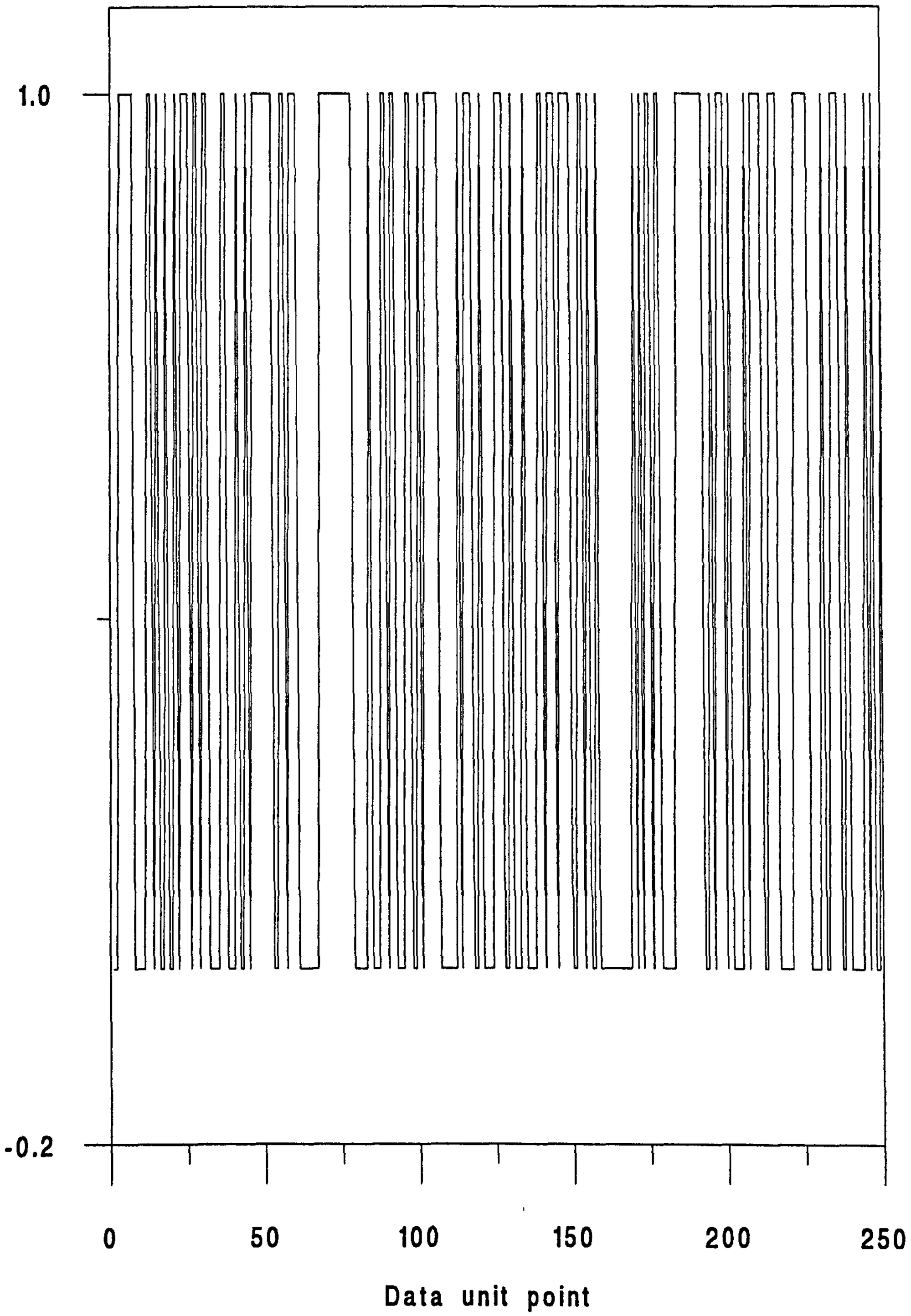


Figure 5.3b: First stage of filtering a weak signal. Many short peaks have been identified as the noise:signal ratio is low, and the threshold for acceptance (the mean) is therefore low.

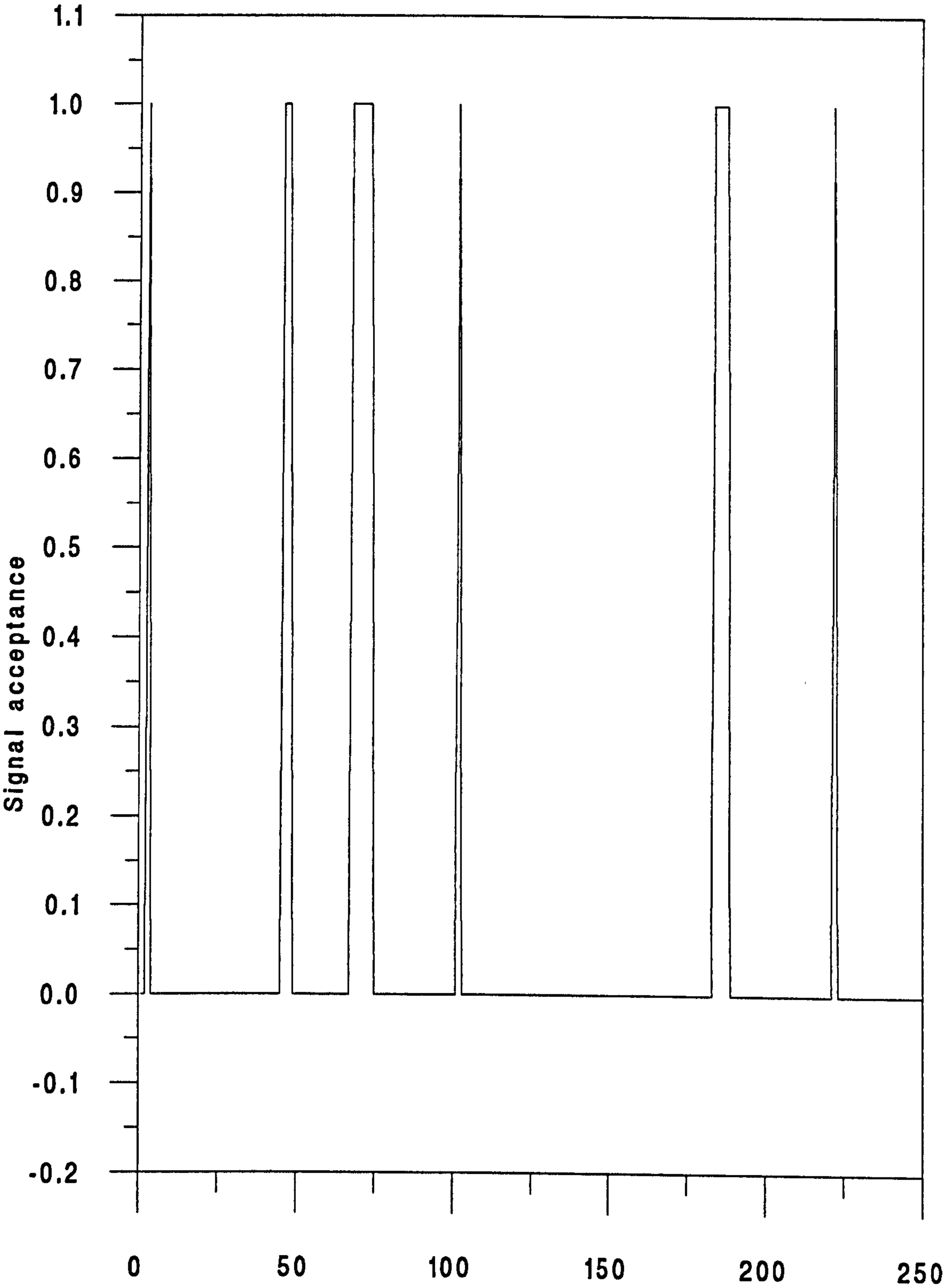


Figure 5.3c: Second stage of filtering a weak signal. Despite removal of many of the bogus peaks illustrated in Figure 5.3b, pulses that do not represent the pulse from the tag have been accepted. The third and fifth peaks represent the tag's pulse.

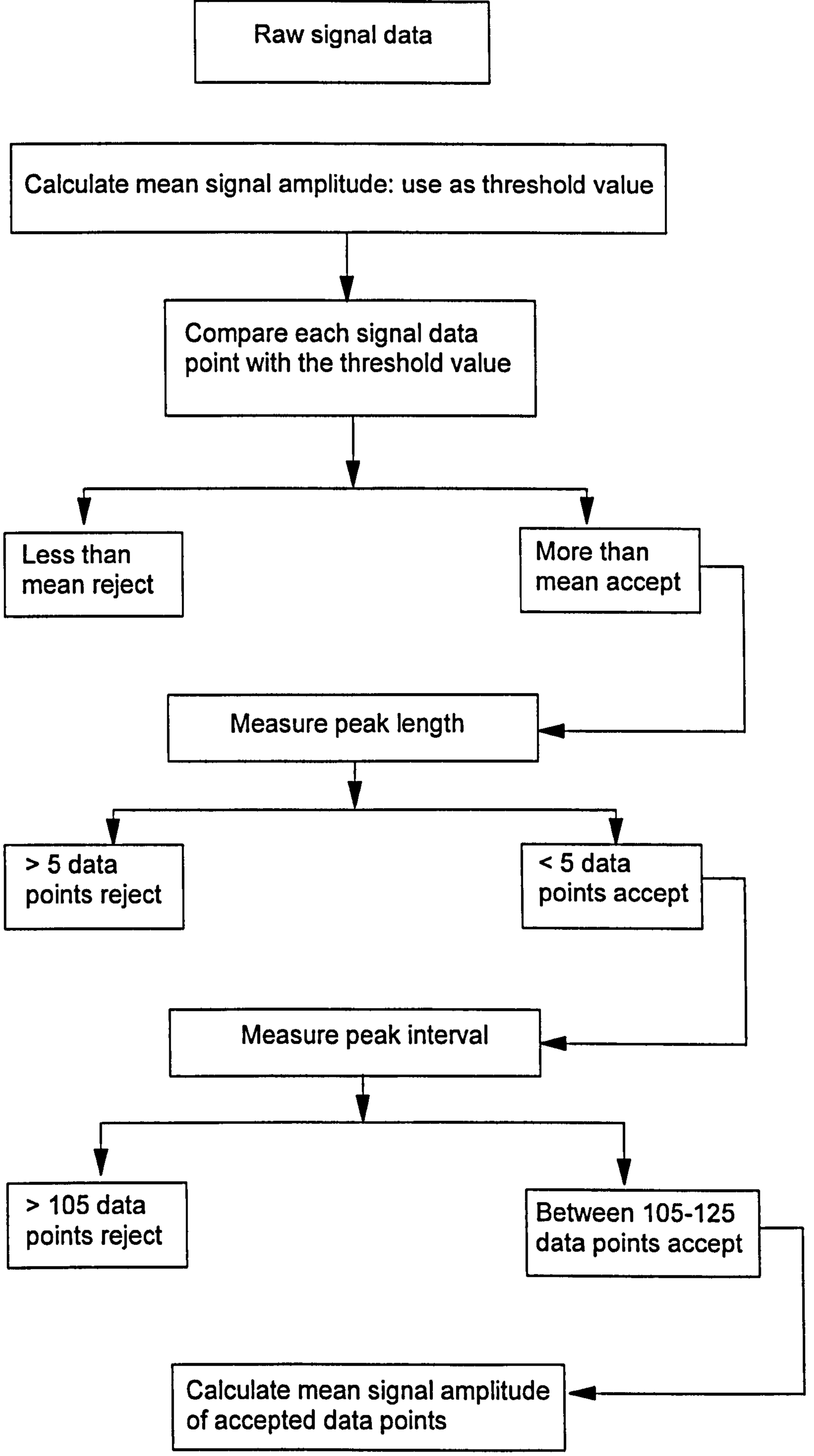


Figure 5.4: Flow chart illustrating the filtering process within the software for the automated system.

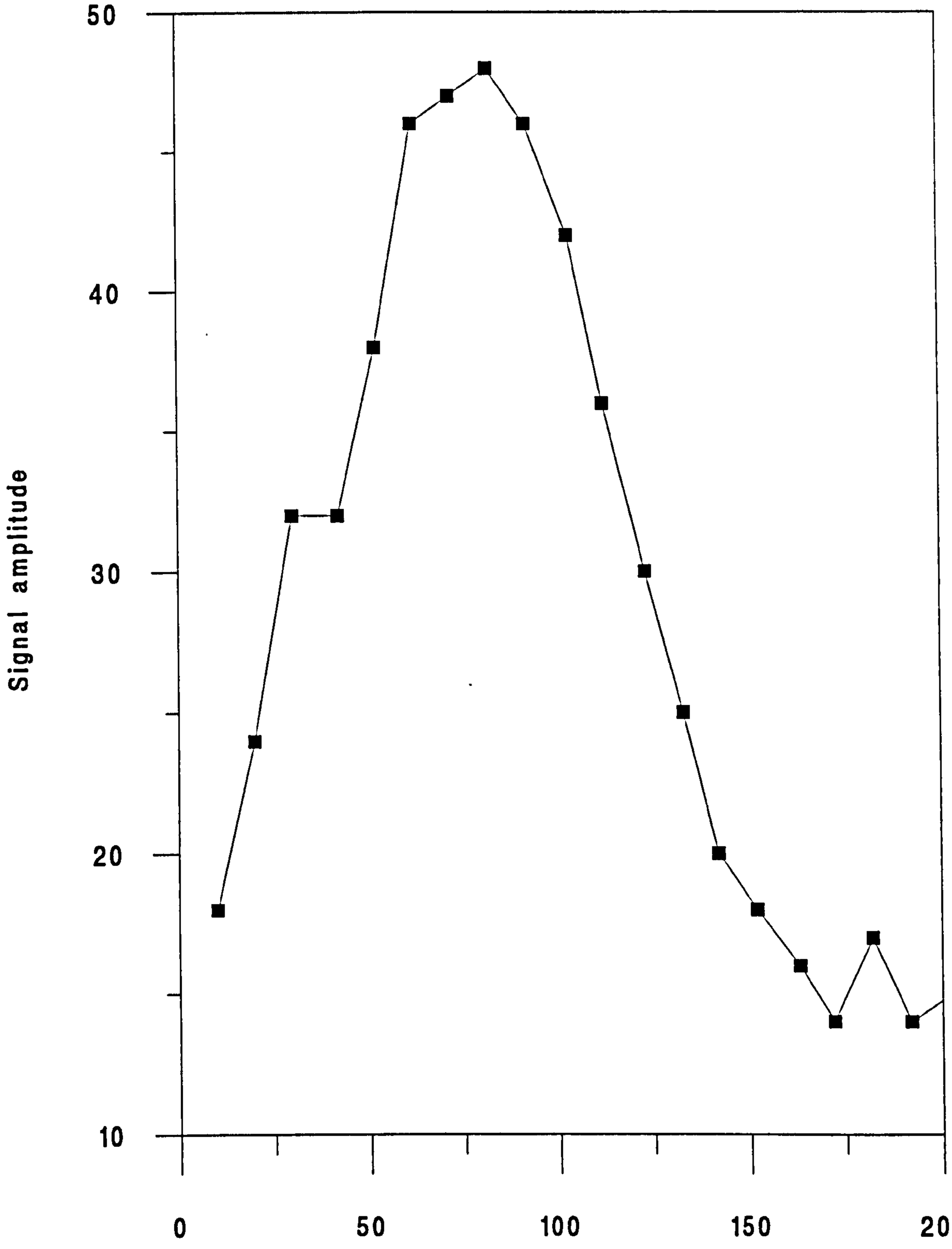


Figure 5.5a: Signal amplitude at stop points of antenna, using filtered data.

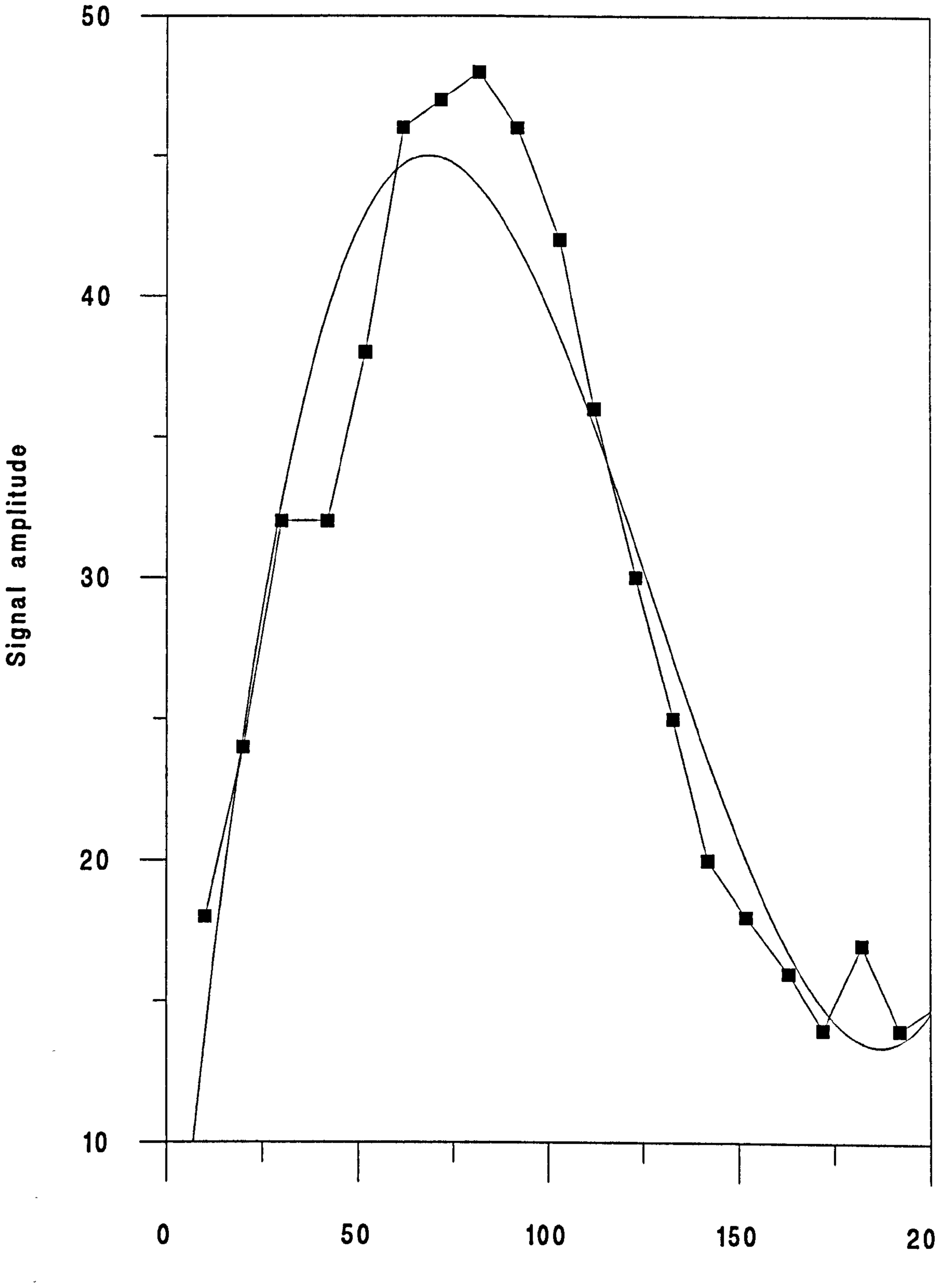


Figure 5.5b: Signal amplitude at stop points of antenna, using filtered data with polynominal line generated from original data. The peak and null location may be identified to the nearest degree.

5.4 Field evaluation of automated system

5.4.1 Introduction

Error is the difference between the true bearing and the bearing estimated by the receiving system and relates to both the accuracy and precision, equation 5.1. Accuracy is a measure of how close a bearing estimate is to the true bearing, precision is a measure of how close replicate bearing estimates are to one another. The common causes of error may be derived from controllable sources, such as the mis-alignment of antennae, biased in receiving systems, tag malfunction or uncontrollable sources, e.g. the impact of distance, terrain, vegetation or weather. Controllable sources can be identified through pilot studies and can be removed, or at least reduced.

Error = True bearing - estimated bearing

(5.1)

The automated system was evaluated by identifying its reception range and the error in bearing estimation. System range was calculated by study of the noise to signal ratio over an increasing distance up to 50m from a receiving antenna. Multiple bearing estimates were obtained for each location to permit calculation of the standard deviation. During winter 1991 and spring 1992, bearing estimates were obtained from over 150 fixes, each with two replicates. Bearing estimates were obtained for tags located at the centre of the enclosure (the release point for the toads), along the perimeter of the enclosure and in a series of sample locations in each of the available habitats. A further sample of bearing estimates was collected where antenna A was 'shaded' by a large sycamore tree. True bearings were gained using a compass at each of the receiving points.

The loss in signal amplitude due to implantation was measured by placing a tag inside the body of a dead toad. The effect of changes in tag orientation on the received signal was also measured; placing a transmitter on a platform at ground level, five metres due north from one of the antennae. The antenna was then rotated until the peak signal was obtained and signal strength then recorded as the tag was rotated through 360°. To provide a three-dimensional image of signal radiation, the tag was

rotated horizontally, laterally and vertically. This was repeated at distances of 10m, 17m and 20m.

5.4.2 Results

5.4.2.1 Signal to noise ratio

The strength of the signal declined over the distance of 50m as predicted under the inverse-square law, Figure 5.6.

The noise level remained consistent over the same distance; therefore the noise to signal ratio decreased over the distance. At distances of only 30m it became difficult to distinguish the signal above the noise.

5.4.2.2 System accuracy and precision

White and Garrot (1990) recommend calculating the error mean to illustrate the level of accuracy of the system, the direction of the mean (either positive or negative) representing the direction of any bias. In a system with no bias the error mean should be equal to zero. While the mean is acceptable it can be distorted, especially when the exceptional values may be recorded, which is likely in triangulation (Springer 1979) and especially using VHF (Priede 1992). Therefore in the current study the median was considered a more appropriate measure to evaluate bias.

For example, Table 5.1 shows bearing estimates collected during trials. The positive error means for both antennae suggest that there was a tendency to under-estimate the bearing. In this individual example, the standard error for antenna A was calculated to be 2.79 and 1.66 for antenna B, indicating a lower precision for antenna A.

White and Garrot (1990) use error histograms of the bearing error to illustrate bearing error and frequency (Appendix 5). In a system with no bias, the error should be consistent and by plotting bearing error and frequency a normal distribution should be produced (Tester 1971). If the system is free from any error caused by directional influences most bearing errors will cluster about zero, the direction of any bias will be identified by the skew of the histogram.

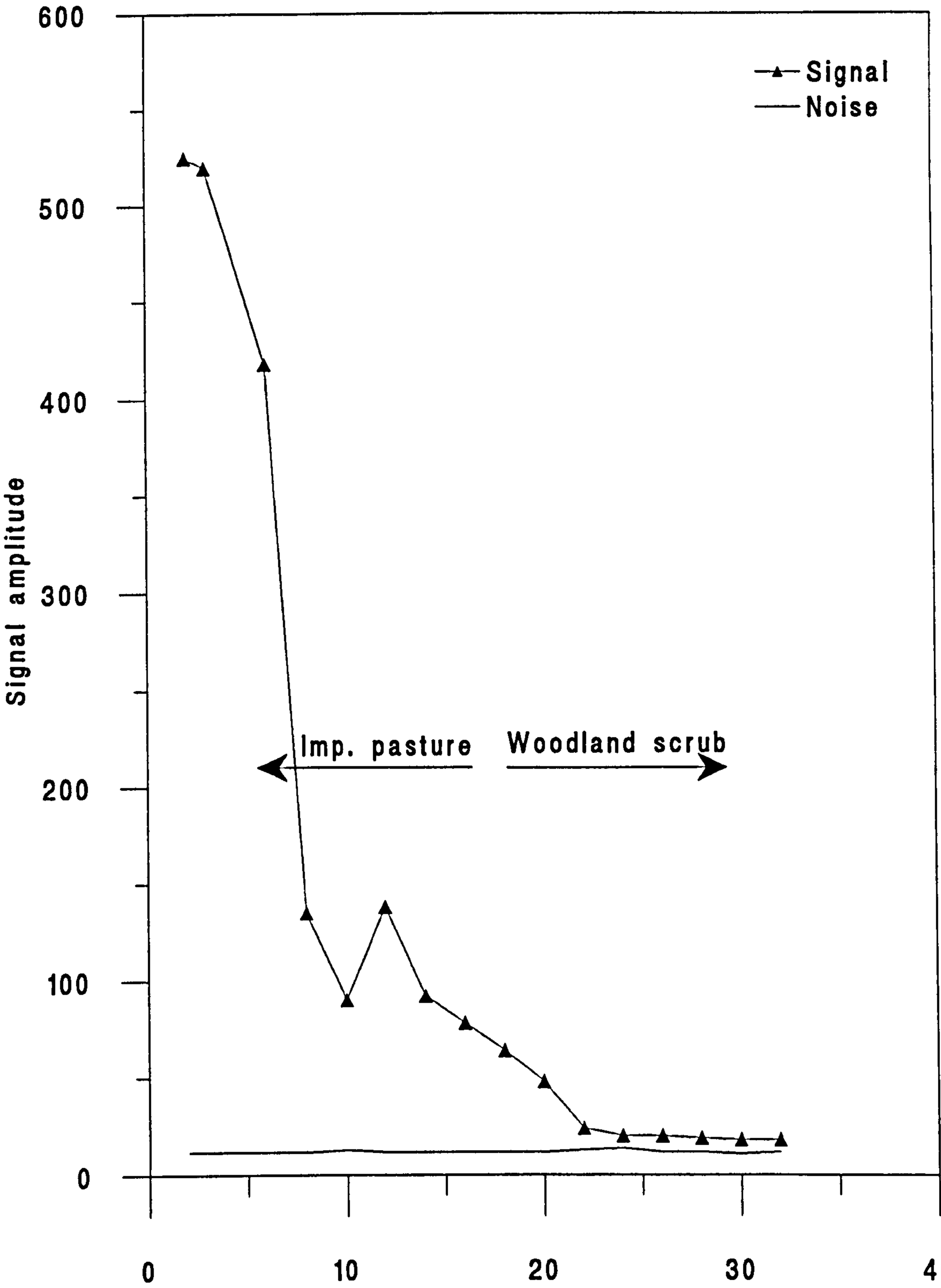


Figure 5.6: Decline in mean (filtered) signal strength with increasing distance from receiving antenna with background noise. Coleorton enclosure, May 1992.

TABLE 5.1: Calculation of mean bearing error for both antennae used as part of the automated system. Units are degrees.

Three replicate bearings were obtained for each of the five test locations. The estimated bearings were obtained from the automated system and the true bearings by compass. In this example, the positive means suggest a slight bias to under estimating the bearing. The median values (1.00° for A and 2.00° for B) confirm this. The standard error of the means (2.79° and 1.66°) suggest that antenna A has a lower degree of precision than B.

True Bearing (t) Antenna A	True Bearing (t) Antenna B	Estimated Bearing (e) Antenna A	Estimated Bearing (e) Antenna B	Error (t - e) Antenna A	Error (t - e) Antenna B
108	90	90	89	18	1
108	90	89	85	19	5
108	90	95	81	13	9
55	120	55	115	0	5
55	120	54	118	1	2
55	120	55	112	0	8
118	90	124	96	-6	-6
118	90	133	76	-15	14
118	90	120	92	-2	-2
28	120	30	125	-2	-5
28	120	40	108	-12	12
28	120	25	115	3	5
162	90	153	89	9	1
162	90	142	94	20	-4
162	90	153	96	9	-6
Mean				**3.67**	**2.60**

TABLE 5.2: Error median and *G* value with decision during trials at Coleorton Autumn 1991 and Spring-Summer 1992. The number of radio-fix location estimates is provided.

(a) Antenna A

Source (N)	Error median	G Value	Decision
Overall (519)	-8.00	62.46	Reject Ho at 0.01. Negative bias
Release (61)	-9.00	8.87	Reject Ho at 0.01. Negative bias
Perimeter (63)	5.00	5.95	Accept Ho. No directional bias
Tree 1 (42)	-22.00	41.97	Reject Ho at 0.01. Positive bias
Tree 2 (42)	0.00	3.16	Accept Ho. No directional bias
Tree 3 (68)	-33.50	28.90	Reject Ho at 0.01. Negative bias
Tree 4 (68)	-15.00	0.79	Accept Ho. No directional bias
Tree 5 (68)	-23.50	13.60	Reject Ho at 0.01. Negative bias
Wood (15)	5.00	3.13	Accept Ho. No directional bias
Rough (6)	1.00	0.34	Accept Ho. No directional bias
Arable (21)	4.00	5.23	Accept Ho. No directional bias
Pasture (15)	1.00	1.64	Accept Ho. No directional bias
Edge (18)	4.50	3.39	Accept Ho. No directional bias

(b) Antenna B

Source (N)	Error Median	G Value	Decision
Overall (519)	0.00	1.21	Accept Ho. No directional bias
Release (61)	-7.00	10.94	Reject Ho at 0.01. Negative bias
Perimeter (63)	-5.00	5.31	Accept Ho. No directional bias
Tree 1 (42)	9.00	41.84	Reject Ho at 0.01. Positive bias
Tree 2 (42)	5.50	14.06	Reject Ho at 0.01. Positive bias
Tree 3 (68)	19.00	76.22	Reject Ho at 0.01. Positive bias
Tree 4 (68)	-70.00	28.98	Reject Ho at 0.01. Negative bias
Tree 5 (68)	4.50	0.22	Accept Ho. No directional bias
Wood (15)	3.00	4.86	Accept Ho. No directional bias
Rough (6)	6.00	6.93	Accept Ho. No directional bias
Arable (21)	1.00	0.53	Accept Ho. No directional bias
Pasture (15)	2.00	1.70	Accept Ho. No directional bias
Edge (18)	-3.50	1.01	Accept Ho. No directional bias

Normality of data can be examined by observation of the histogram curve, with 70% of the data falling within the range set by the mean ± the standard deviation (Fowler and Cohen 1992). However, comparison of the number of positive and negative bearing errors was completed to test for normality using the *G*-test (Fowler and Cohen 1991). If the true bearing is represented by an error of 0°, in a system with no bias the positive bearing errors should equal the negative bearing errors. Bearing errors were assigned a positive value between 1-180° clockwise, and a negative value between 1-180° anti clockwise (Hupp and Ratti 1984). Tables 5.2a and 5.2b show the medians and *G* scores for each group of results.

The *G* values were calculated for the combined set of location estimates used in the assessment exercise (over 500 fixes). The *G* value of 62.46 for Antenna A was highly significant ($P < 0.01$) which indicates a departure from a purely random error distribution. The data suggest that Antenna A lacked accuracy, with a bias towards over-estimating the bearing, producing a negative error, underlined by the median value of -8.7. On the other hand, the *G* value for Antenna B was 1.212, which is not significant, indicating higher accuracy since the distribution of bearing errors was uniformly about zero. The median value for this data set was 0 indicating uniformity in error distribution.

5.4.2.3 Tag orientation and implantation

Attenuation with horizontal orientation and range is shown in Table 5.3 and Figure 5.7. The signal pattern at 5, 10 and 20m is relatively consistent, at 17m there appears to be some distortion possibly due to a change in the local reflectivity of the vegetation. Results in the three dimensions are shown in Table 5.4 and in Figures 5.8 and 5.9.

Implantation into the stomach of a dead toad reduced the radiated power. The reduction in power was similarly influenced by orientation, as discussed above, and ranged between 4 and 45% (mean 23 ± 7%), Table 5.5.

TABLE 5.3: Changes in signal amplitude due to tag orientation in the horizontal plane. Amplitude figures are in unclassified units based on an increasing scale.

Tag orientation (° from origin)	Distance from receiving antenna in metres (Signal amplitude from receiving antenna)			
	5	10	17	20
0	157	138	32	16
30	176	148	43	17
60	181	153	52	19
90	181	152	53	20
120	175	145	32	17
150	170	145	25	17
180	152	139	28	16
210	145	137	22	16
240	146	135	22	15
270	149	131	20	15
300	152	137	19	17
330	153	141	19	15
360	159	142	20	16
Highest	181	153	52	20
Lowest	145	131	19	15
% Variation	20%	15%	60%	25%

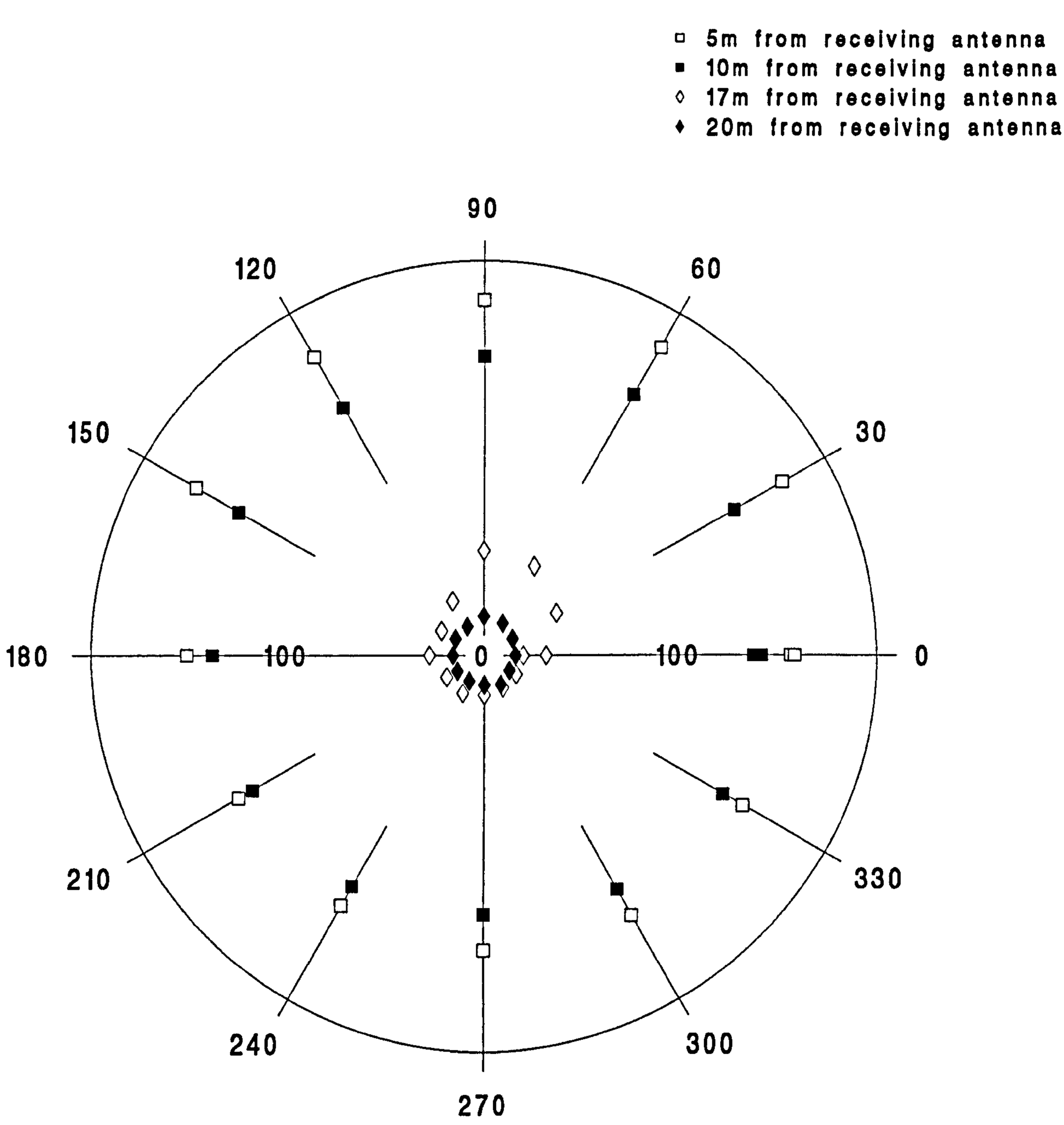


Figure 5.7: Effect of horizontal orientation of tag on attenuation at an incresasing distance from the receiving antenna.

TABLE 5.4: Variation in signal amplitude under 2-dimensional rotations. Amplitude figures are in unclassified units based on an increasing scale.

Tag orientation	Signal amplitude (at 10m from antenna)	
	Lateral roll	Vertical flip
0	61	39
30	89	44
60	86	57
90	30	58
120	16	51
150	20	48
180	51	50
210	63	47
240	52	41
270	45	37
300	55	31
330	76	27
360	64	35
Highest	89	207
Lowest	16	2
% Variation	82%	99%

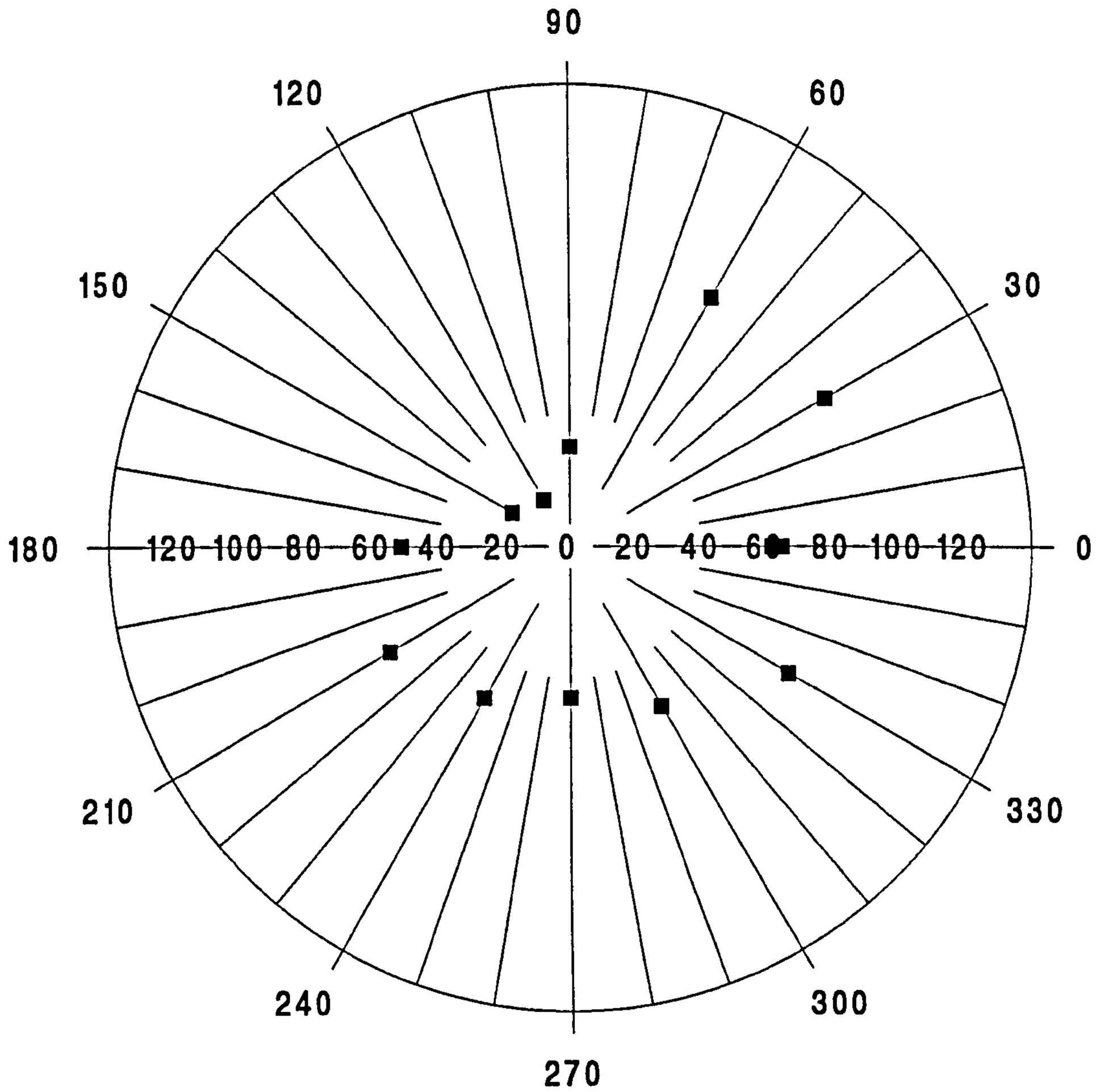


Figure 5.8: Effect of 'lateral roll' on signal attenuation. Tag at 10m from receiving antenna.

TABLE 5.5: Variation in signal amplitude following implantation of a radio-tag into the stomach of an adult toad. Amplitude figures are in unclassified units based on an increasing scale.

Tag orientation (° from origin)	Signal amplitude		
	Extemal	Implantated	% variation
0	45	39	13%
30	51	44	14%
60	70	57	19%
90	74	58	22%
120	66	50	24%
150	59	52	12%
180	52	50	4%
210	50	47	6%
240	57	41	28%
270	54	37	32%
300	54	31	43%
330	49	27	45%
360	47	27	43%
Mean variation (with standard error) %			23 ± 7%

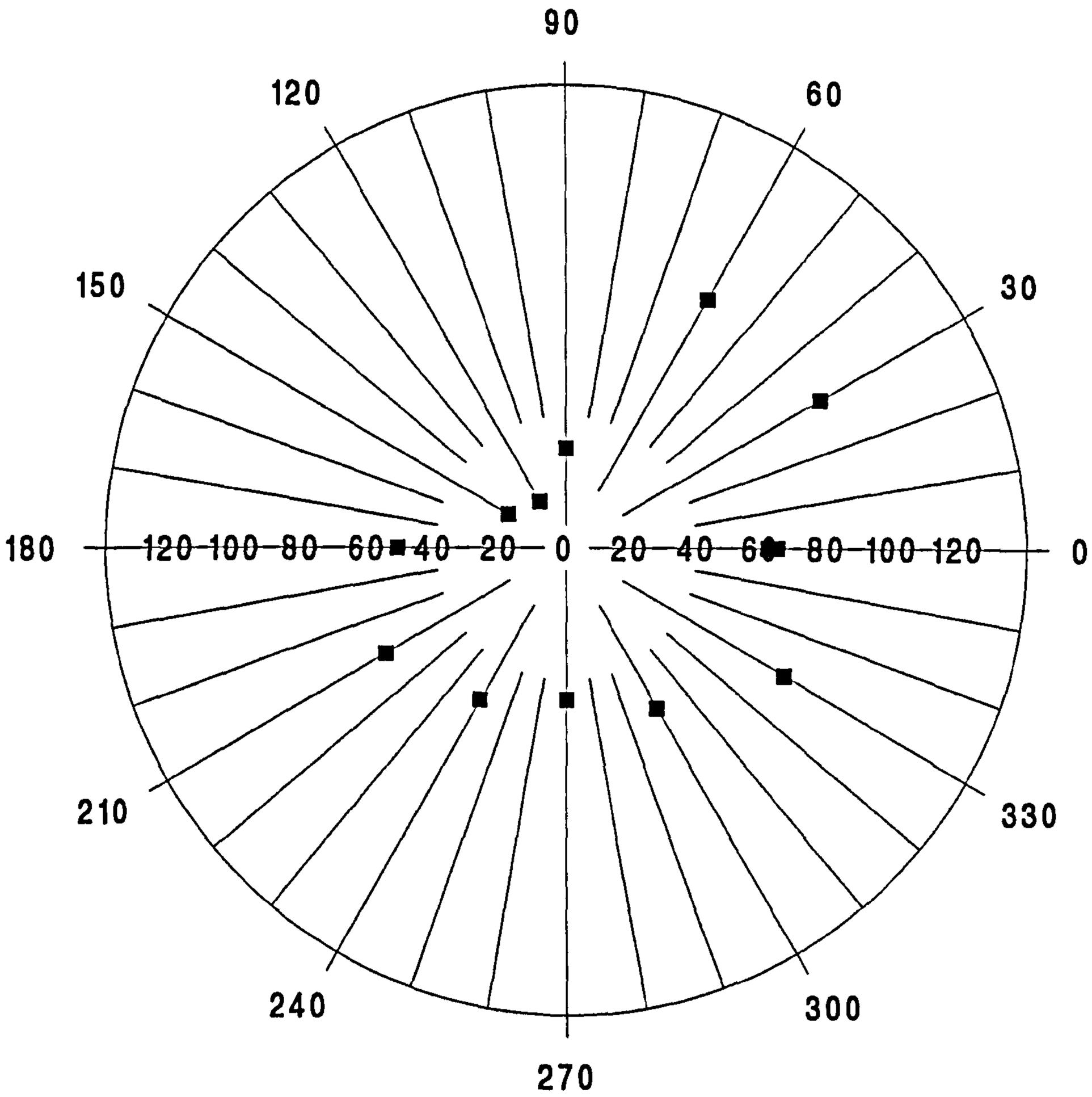


Figure 5.8: Effect of 'lateral roll' on signal attenuation. Tag at 10m from receiving antenna.

5.5 Discussion

5.5.1 System function

The software permitted the control of the system without the need of a dedicated researcher, although day to day checks were required. The simple filtering system enabled identification of a weak signal from a noisy background, although the initial signal strength was important in successful signal identification. The major difficulty in signal identification was the low signal to noise ratio. The problems associated with a low ratio-between signal and noise could only be reduced by the development of a new tag that could produce a higher power signal.

5.5.2 System accuracy and precision

It is likely the bias observed for antenna A was caused by mis-alignment between the grid and the antenna. This antenna was in a more exposed location than B and liable to be influenced by strong winds. Location estimates close to the sycamore tree (Tree locations 1-5 in Tables 5.2a and 5.2b) showed high *G* values and bearing errors indicating the influencing of the tree. The release point was also slightly shaded by trees and this was reflected by similar bearing inaccuracies. Transformation of equation 5.1 shows that the bearing estimate for each antenna consists of the true bearing plus the error, equation 5.2. The total error can be positive or negative.

$$\textbf{Bearing estimate} = \textbf{true bearing } (\pm) \textbf{ total error} \tag{5.2}$$

Confidence limits may be created based on this error with the original location estimate forming the centre of a polygon produced by the bisection of the bearings from each receiving point and confidence interval (Springer 1979). Transformation of equation 5.2 with standard errors produces the four corners of the error polygon (Heezen and Tester 1967), equation 5.3. This places puts a limit on the grain of the location estimation abilities.

$$\textbf{Bearing estimate} = \textbf{bearing estimate} \pm (1.96 * \textbf{standard error}) \tag{5.3}$$

Standard error for antenna A was +/- 1.47, and +/- 1. 55 for antenna B, indicating that the antennae had similar precision in location estimations and represents the generalised bearing error for the system. These errors are lower than those quoted in previous studies; Springer (1979) cites an error of +/- 3.9, whilst Schober *et al.* (1984) cite an error of +/- 8 (cited in Kenwood 1989).

Accuracy in the location estimates was required to be sufficient to minimize the number of locations where the error polygon includes the boundary between two habitat types. The maximum error polygon size that could occur within the enclosure was calculated as 14.2m². The smallest habitat was the hedge, although the overall size of the habitat (34m²) was larger than the maximum error polygon its linear nature puts doubt on the confidence of location estimates placed inside the hedge. The remaining habitats are sufficiently large to reduce this problem (wood 165m², cultivated 205m², improved grassland 207m² and rough grassland 222m²). The data collected by daily hand tracking were used to supplement the automated data where there was doubt.

The bearing errors observed during tests of the automated system were comparable to those in other hand tracking studies, where the observer had the benefit of continuous involvement (Springer 1979, Priede and Swift 1992). Errors occasionally did develop during the functioning of the system, illustrated by the directional bias that occurred when antenna A moved out of alignment with the grid. Evidence of signal reflection and absorption was illustrated by the impact of intervening trees. This is a difficulty recognised using VHF (Priede and Swift 1992) which cannot be rectified.

Orientation of the tag in the horizontal plane illustrated variation in signal amplitude of up to 62%, although the size of this variation declined with increasing overall signal power closer to the receiving antenna. This effect is likely to be greatest in the study of small and highly mobile animals, especially if the transmitters are free to rotate. It would be difficult to control orientation of the ingested transmitters used in the current study after deployment. To reduce the problem the tag design would need to ensure that the radiation pattern of the signal from the tag was uniform.

Chapter Six: Characteristics of the breeding migration and metamorph emergence, Osbaston Hall Estate in relation to habitat (1991-1994)

6.1 Introduction

This chapter discusses the data obtained during the current study through intensive pitfall trapping during the breeding migrations, and during metamoprh emergence at Osbaston Hall, Leicestershire (1991-1994). These studies are complemented by additional research at Little Wittenham Nature Reserve, Oxfordshire (1994-1995).

The breeding migration has been an important element of a number of studies on the population dynamics of the toad, providing the best opportunity to sample a large number of animals, study migration routes and behaviour, and to complete recapture exercises for population estimates (notably work by Gittins *et al.*, Reading and Clarke 1995, see Chapter 1). The characteristics of metamorph emergence during the late summer have been studied in less detail (with the main exceptions of Paull, Wisniewski and Slater, 1981 and Oldham and Swan 1991), although data from this life stage are essential for a full understanding of the population dynamics of the species.

The specific objectives for the current study, addressed in this Chapter, are three fold; first, to compare the spatial distribution of toad catches from a series of contrasting habitats within and between study years. This was achieved through a series of drift fences and Habitat Specific Enclosures (HSEs). Secondly, to establish any variation that may occur within the population in terms of body condition, survival and length in individuals generating from contrasting habitats within and between study years. On capture animals were weighed and measured; condition was expressed as a relationship between mass and length (Kuhn 1994). Toads were given a Panjet mark, to represent the year of capture, and a toe-clip to represent the catch habitat. Although this did not provide individual recognition, recaptured toads provided information on the relative benefits of each habitat, through comparison of growth, condition, survival and fecundity. Thirdly, research aimed to determine the effect of the distance from the breeding on the spatial distribution of catches in the various habitats. This was achieved by the specific design of the field experiment at Little Wittenham Nature Reserve.

The output of metamorphs from both of the ponds at Osbaston Hall was estimated to establish breeding success and to provide data for population studies (Chapter 8). This was achieved through continuous sampling throughout the emergence period, then estimating the total output of metamorphs through extrapolation.

6.2 Definitions of terms

For each year, days have been numbered consecutively using January 1st as day 1.

The *gross catch* represents all toads intercepted by the drift fences, including the outside and inside of the enclosures, and all immediate re-captures (i.e. recaptured within the same year) in any one year. The gross catch has been sub-divided into each habitat using the number of toads caught per drift fence or HSE, and the number of toads caught per metre length of fence (toads/m).

The *daily catch* represents the combined catch from all pitfalls for each day of the breeding season.

The *nett catch* represents only those toads caught *inside* the HSE and those on the *distal* side of the drift fences, i.e. the opposite side to the breeding site. Where possible, toads known to have evaded the fences, as identified by their tag and 'trespassed' into other habitats, immediate recaptures, and those placed into the enclosures as part of the fence efficiency trials were removed from the nett catch.

Trapping effort was expressed in terms of the number of animals caught per metre length of fence (*toads/m*). Traps were placed at a standard distance of 10m apart for each drift fence and within each HSE. The design of the HSEs did not permit direct comparison of catches within the HSE to those from the drift fences. The HSE catches are from a restricted catchment, whilst the drift fences intercept animals from a wider vicinity. The catches from the outer traps of the HSE were compared, with the diameter of the HSE representing its length.

The *breeding migration* describes the movement of adult toads from the terrestrial habitat to the breeding site during the spring.

The timing of the migration is defined each year by the *median date of activity*, i.e. the date by which 50% of the gross catch for that year has been caught in the traps (Slater, Gittins and Harrison 1985).

The *active duration* of the season refers to the number of nights on which there was substantial toad movement, defined as when the pitfall catch represented at least 1% of the gross catch for that year (Gittins 1983a).

Condition is expressed through an index between body length and mass (Kuhn 1994) and used to described the health of individual toads.

The *night count* refers to the number of toads observed in the breeding pond per evening, and is an indication of the size of breeding population on the given evening. Night counts have been used to describe the size of an adult population for conservation purposes (NCC 1989).

The *sex ratio* is expressed as the proportion of males to females derived from the nett catch.

Gross metamorph catch represents the number of metamorphs caught in the all traps for a given season and expressed for the Lake and Spur.

Total emergence is defined as the estimated number of metamorphs leaving the breeding site based on an extrapolation from the gross metamorph catch. This extrapolation uses the total sampling length, defined as the sum of the widths of each trap, and the perimeter length of each breeding pond. This ratio was then used to extrapolate the gross metamorph catch representing the total emergence. The variation in catch between the individual traps was used to provide a confidence interval for the estimated total emergence.

6.3 Results

6.3.1 Breeding migrations 1992-1994

The pitfall traps for each the fences at Osbaston Hall were opened by 1st March in each year of the current study. During the autumn of 1992 the HSEs were constructed around the Wood to the north of the lake (WDI/WDO) and in the Rookery (RKI/RKO) and Poplars (PPI/PPO). Habitat codes and fence descriptions are listed in Table 6.1. The location of the fences in each year of the current study are shown in Chapter 3 and detailed in Appendix 4. Night counts in the two breeding ponds were conducted on a nightly basis once the evening temperatures had risen to over 5°C and the catches in the terrestrial traps had indicated that migration had commenced.

6.3.1.1 Temporal distribution of toad catches

The temporal distribution of daily catch (both males and females) over the breeding season for each of the three years is shown in Figure 6.1a - 6.1c. Peaks in migration, represented by catches in the pitfall traps, coincided with warmer evenings. Few toad catches at the pitfall traps were observed to occur when minimum air temperatures fell below 4°C, Figures 6.2a - 6.2c. The continuity of the movement was interrupted when temperatures fell below this threshold, with the migration delayed until temperatures rose to above 4°C for a series of consecutive evenings, for example during days 81-96 in 1992, Figure 6.2a. Further analysis of the role of weather conditions and toad migration is provided in Appendix 6.

The timing of the female migration was always later than that of the males'. The median date of activity varied for the males between the years by only 6 days (day 77 to 83), while the female breeding migrations varied by 13 days Table 6.2. The active duration of the breeding season in 1992 was over the twice the length recorded in 1993 and 1994, during this year the timing of the female migration was also proportionally later than that of the males, Table 6.2.

Peak night counts at the breeding site were associated with the timing of the male migration. Night counts for the eastern bank (LE), western bank (LW) of the Lake and for the western bank of the Spur (SW) over 1992-1994 during March and April are

TABLE 6.1: Codes, description and operational period for toad fences used at Osbaston Hall, 1992-94. Location of fences is shown in Chapter 3.

Fence line	Code	Style	Distance from pond	Fence length	Number of pitfalls
Spinney	SP	Drift	400	100	10
Arable West	AW	Drift	100	100	10
Arable North	AN	HSE	210	150	13
Rough Wood	REW		175	70	11
Rough Field	REF		125	80	5
Rough Inner	REI		160	80	27
Hedge Arable/Rough	HDI		200	150	30
Rookery (inside)	RKI	HSE	250	200	20
Rookery (outside)	RKO		275	100	12
Poplar Central (inside)	PPI	HSE	25	200	20
Poplar Central (outside)	PPO		50	100	12
Poplar North (inside)	PNI	HSE	25	60	6
Poplar North (outside)	PNO		25	30	3
Poplar South (inside)	PSI	HSE	25	60	6
Poplar South (outside)	PSO		25	30	3
Wood (inside)	WDI	HSE	175	210	28
Wood (outside)	WDO		175	210	15
Hedge Arable (inside) A	HAI A	HSE	50	100	10
Hedge Arable (outside) A	HA0 A		50	100	10
Hedge Arable (inside) B	HAI B	HSE	200	100	10
Hedge Arable (outside) B	HA0 B		200	100	10
Hedge Arable (inside) C	HAI C	HSE	350	100	10
Hedge Arable (outside) C	HA0 C		350	100	10

Figure 6.1a: Temporal distribution of males and females caught during the 1992 breeding season, Osbaston Hall.

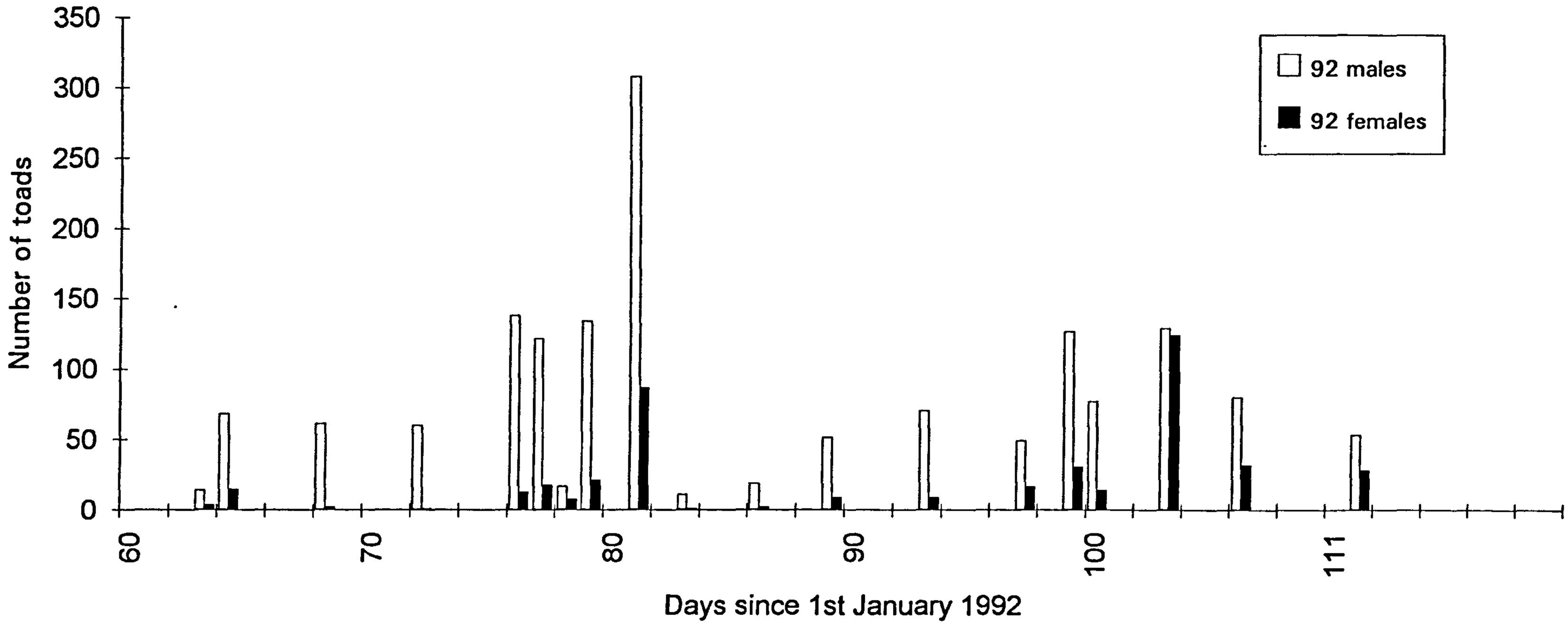


Figure 6.1b: Temporal distribtion of males and females caught during the 1993 breeding season, Osbaston Hall

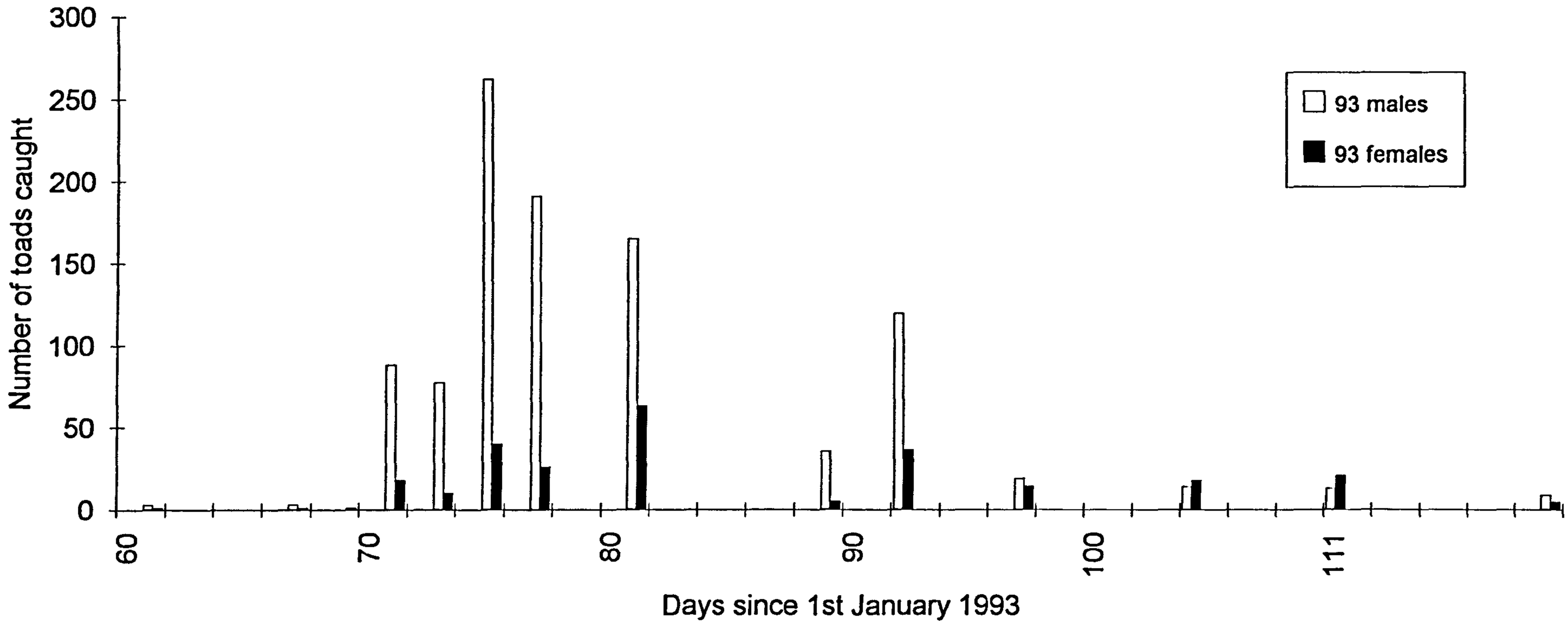


Figure 6.1c: Temporal distribution of males and females caught during the 1994 breeding season, Osbaston Hall.

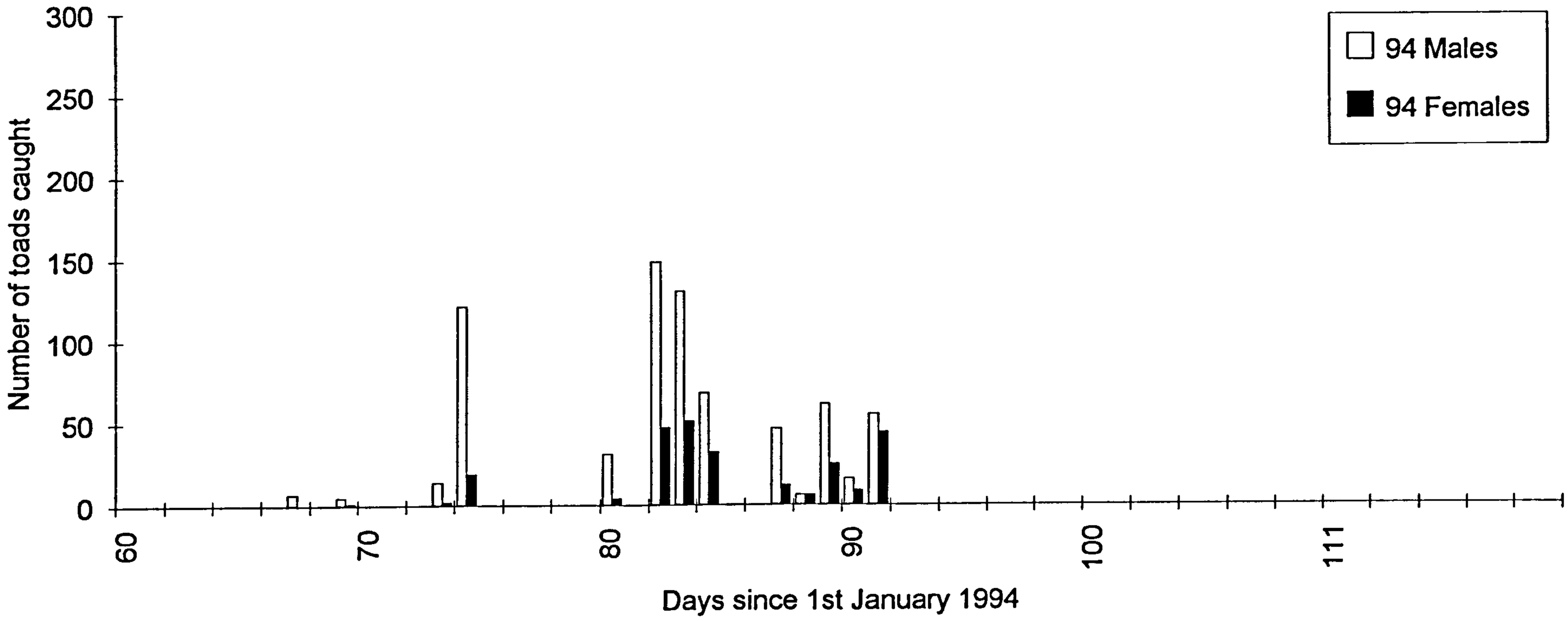


Figure 6.2a: Variation in gross toad catch (males and females) and air temperature, as measured on site with a whirling hygrometer, Osbaston Hall 1992. Days are numbered consecutively from 1 January, temperature is in degrees centigrade.

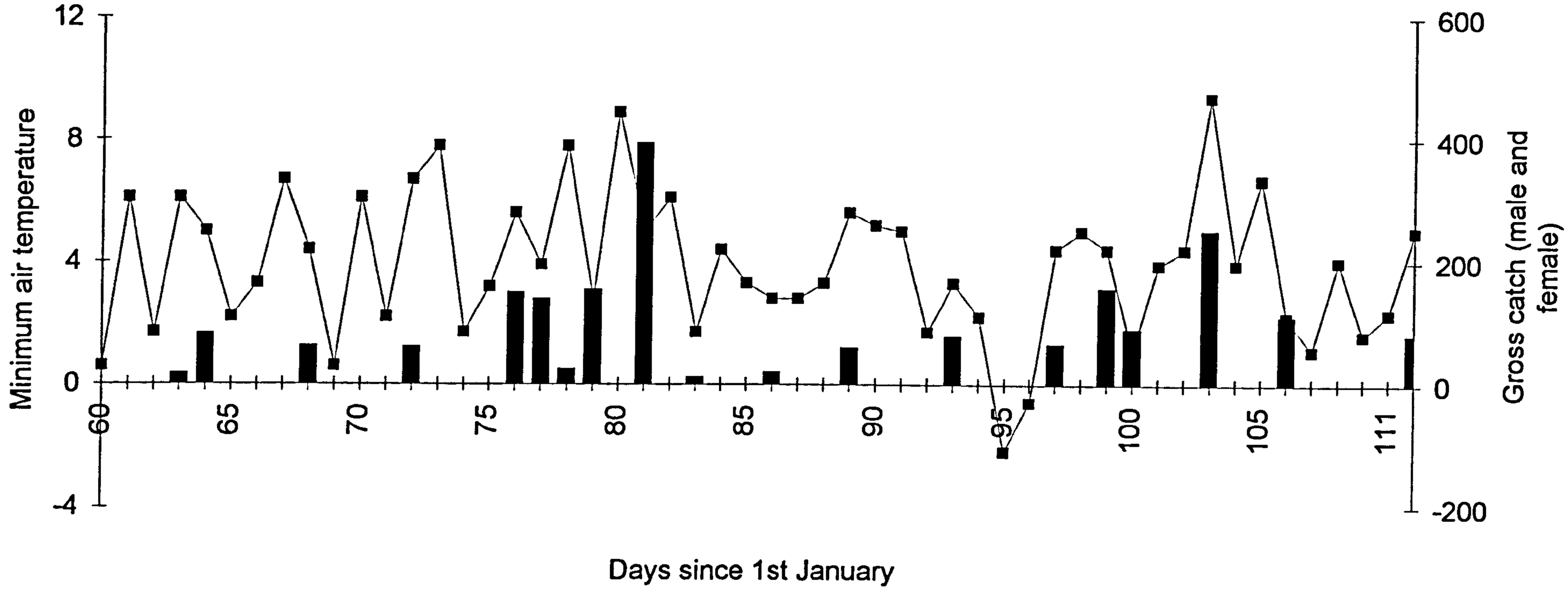


Figure 6.2b: Variation in gross toad catch (males and females) and air temperature, as measured on site with a whirling hygrometer, Osbaston Hall 1993. Days are numbered consecutively from 1 January, temperature is in degrees centigrade.

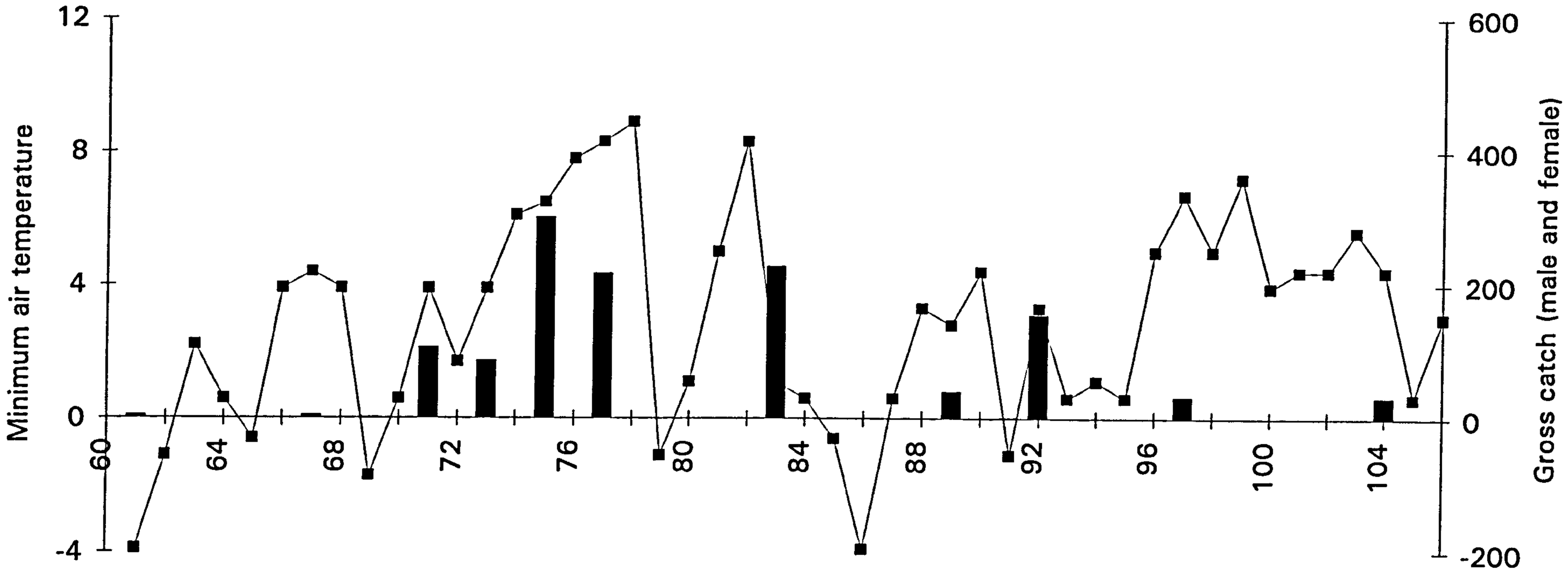


Figure 6.2c: Variation in gross toad catch (males and females) and air temperature, as measured on site with a whirling hygrometer, Osbaston Hall 1994. Days are numbered consecutively from 1 January, temperature is in degrees centigrade.

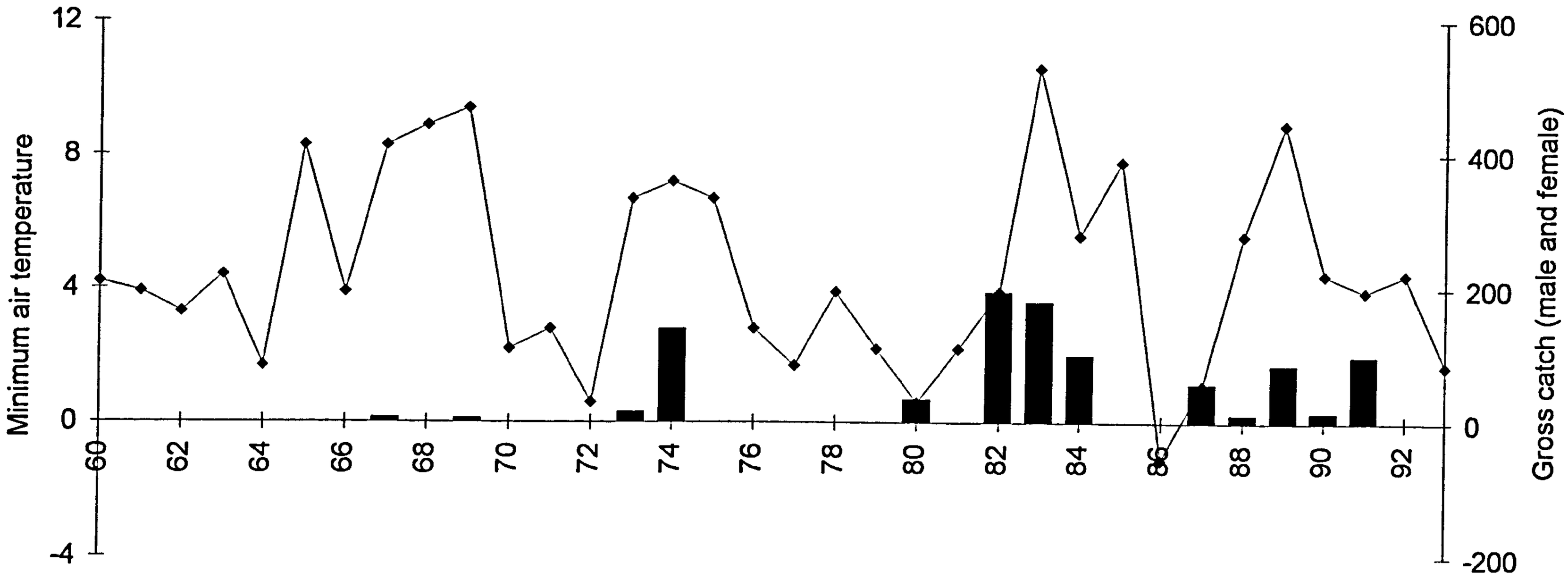


TABLE 6.2: The timing and duration of the toad migration at Osbaston Hall Estate, 1992-1994. Trapping period and timing of migration recorded in days in January 1st. 1: The timing of migration is referred to in terms of the median date of activity, which is defined as the date by which 50% of the total number of toads caught that year had been counted (Slater, Gittins and Harrison 1985). 2: The active duration refers to the number of nights on which substantial toad movement occurred, based as a capture of at least c.1% of the estimated population (Gittins 1983a), based on an adult population of 5000.

Year	Trapping period	Timing of migration[1]		Active duration[2] (Days)	First spawning
		Males	Females		
1992	63 - 118	81	97	13	100
1993	50 - 89	77	84	6	85
1994	67 - 93	83	89	6	87

TABLE 6.3: Inter-year variation in size and date of peak water count for both water bodies, Osbaston Hall 1992-1994. 1: Count period and date of peak water count in days since 1st January. Date of peak water count for single males and pair provided in parenthesis.

Year	Count period	Peak water count (toad counted in the water body)					
		Lake west		Lake east		Spur west	
		Males	Pairs	Males	Pairs	Males	Pairs
1992	85 - 102	280 (100)	54 (101)	250 (100)	57 (101)	182 (100)	34 (102)
1993	74 - 107	142 (81)	49 (83)	152 (81)	27 (81)	194 (81)	62 (83)
1994	74 - 95	197 (89)	82 (89)	74 (91)	29 (89)	292 (89)	101 (89)

shown in Figures 6.3a - 6.3c. The number of males counted on both LW and LE declined over 1992-1994, Table 6.3. The peak count on the eastern bank in 1994 represented only 30% of the 1992 count. The number of males counted on the west bank of the Spur (SW) in 1994 showed an increase of 60% compared to the 1992 count. While the number of pairs counted on LE declined by 50% over the three years, the number of pairs on LW and SW increased, with the decline most noticeable on SW, Table 6.3.

The night counts at the breeding site during the current study were heavily biased towards males in each year. The sex ratio was observed to decline on each bank over the course of the breeding season, Figure 6.4. First spawning in 1992 (Day 100) was later than in both 1993 (Day 85) and 1994 (Day 87). First spawning occurred close to the date of the peak night count, but was obviously related to the timing of female migration, Table 6.2.

6.3.1.2 Spatial distribution of toad catches

The gross catch in 1992 was 1726, the number of toads caught at each fence is shown in Table 6.4. The spatial distribution of the nett catch for each habitat during the 1992 breeding influx is shown in Figure 6.5. Twenty-seven percent of the nett catch was caught at the fence lines outside of the Rough East Complex (REW and REF), located 200m from the pond. Twenty percent was caught inside the Poplar Plantation HSE (PPI), less than 25m from the breeding site and 15% of the nett catch was caught inside the Rookery HSE (RKI). Over 50 toads (4%) were caught at the drift fence at the Spinney (SP), located 400m away from the breeding site. The drift-fences in the arable fields (AW and AN) provided 20% of the nett catch.

The gross catch in 1993 declined slightly (1249 toads), from the previous year, Table 6.4. For the nett catch the largest number of toads was caught inside the Poplar Plantation HSE, representing 51% of nett catch, Figure 6.6. The traps at Rough East Complex were not functional in 1993, although the hedgerow between the pasture field and the northern arable field remained, and was fenced off to represent a hedge HSE (HDI). Two small circles, Polar North (PN) and Poplar South (PS), were constructed as part the fence efficiency trials.

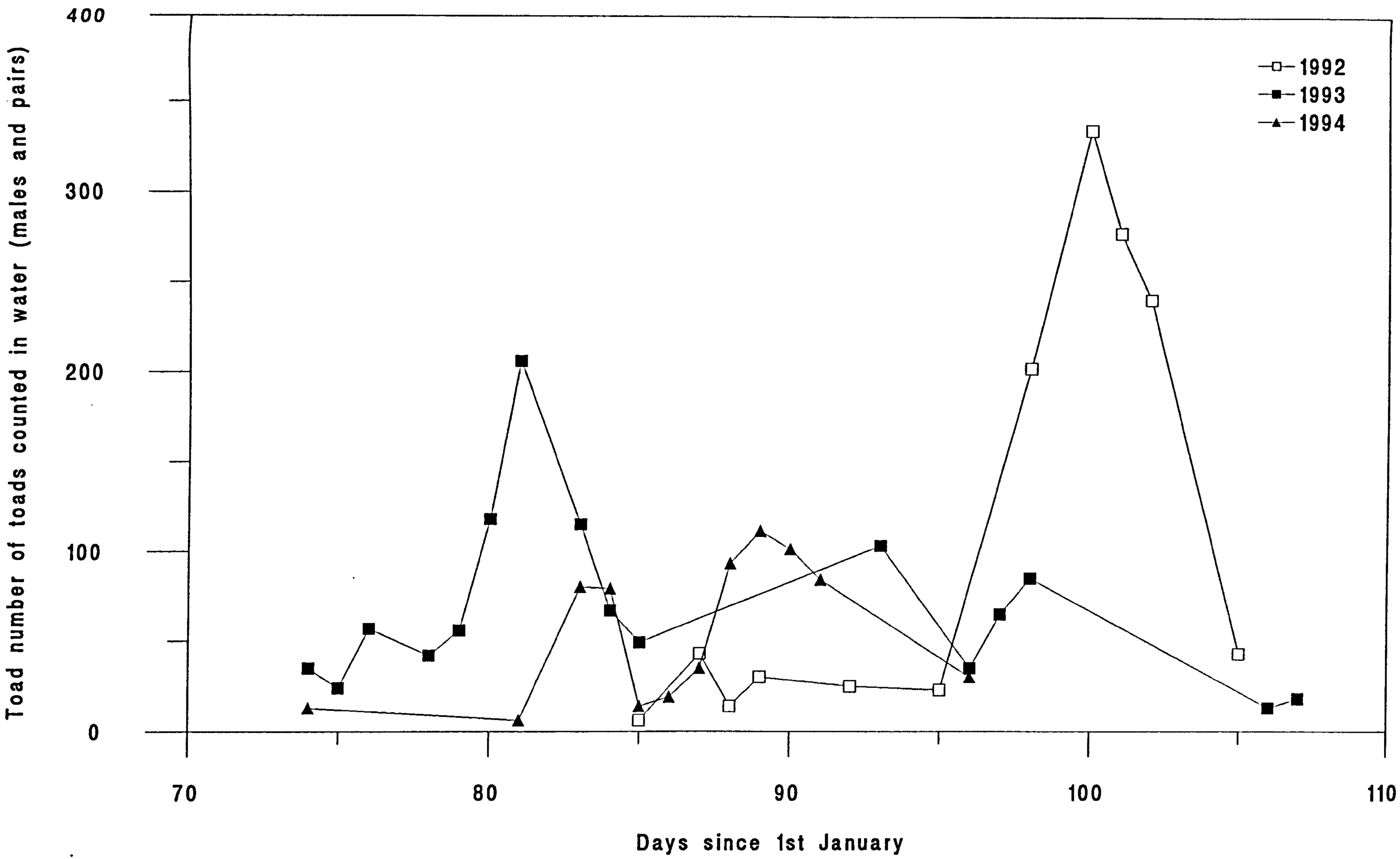


Figure 6.3a: Total number of toads (both males and pairs) counted on Lake East (LE) during the course of the breeding season. Osbaston Hall 1992-1994.

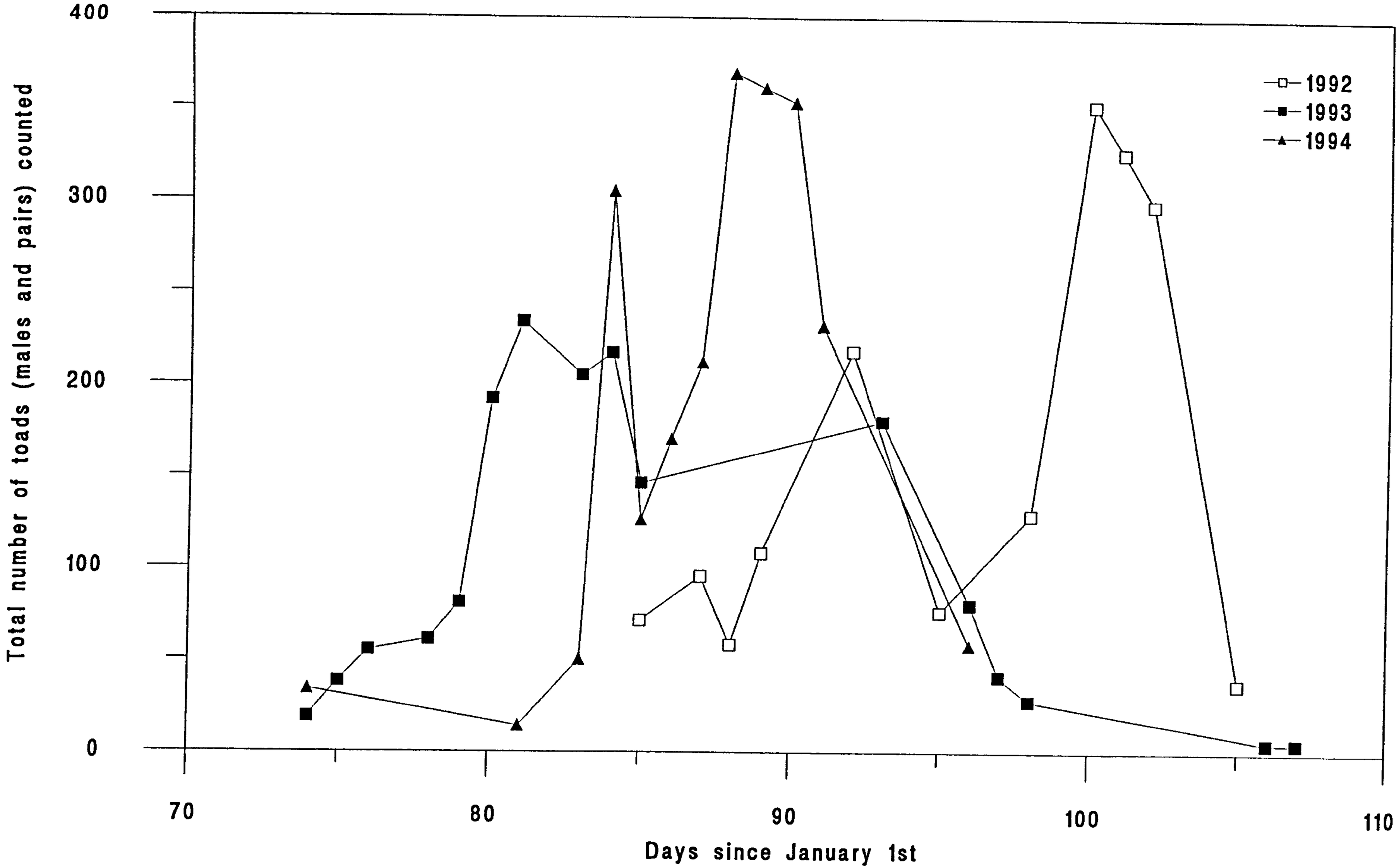


Figure 6.3b : Total number of toads (males and pairs) counted on Lake West (LW) during the breeding season, Osbaston Hall 1992-1994.

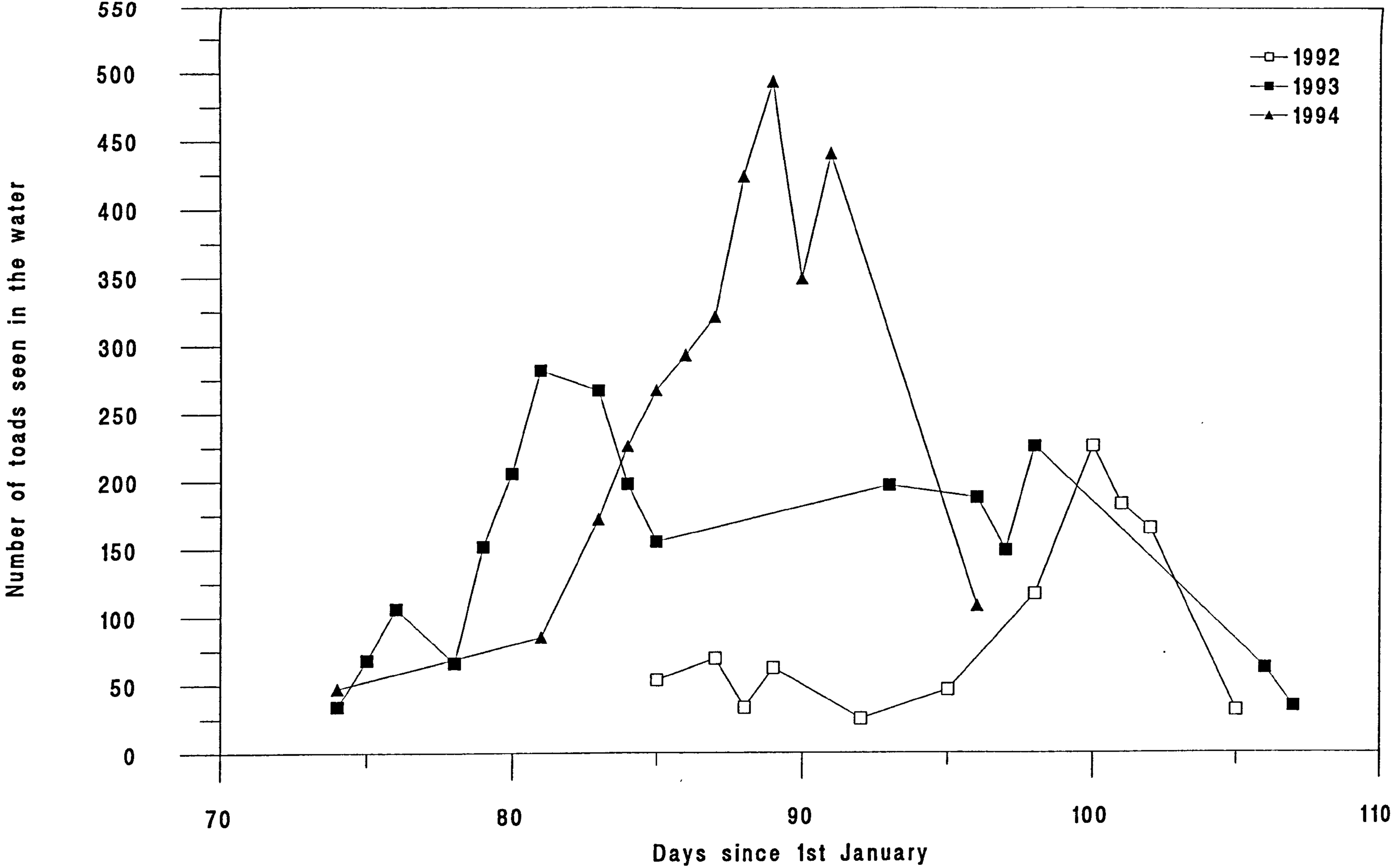


Figure 6.3c: Total number of toads (males and pairs) counted on the western bank of the Spur during the breeding seasaon, Osbaston Hall 1992-1994.

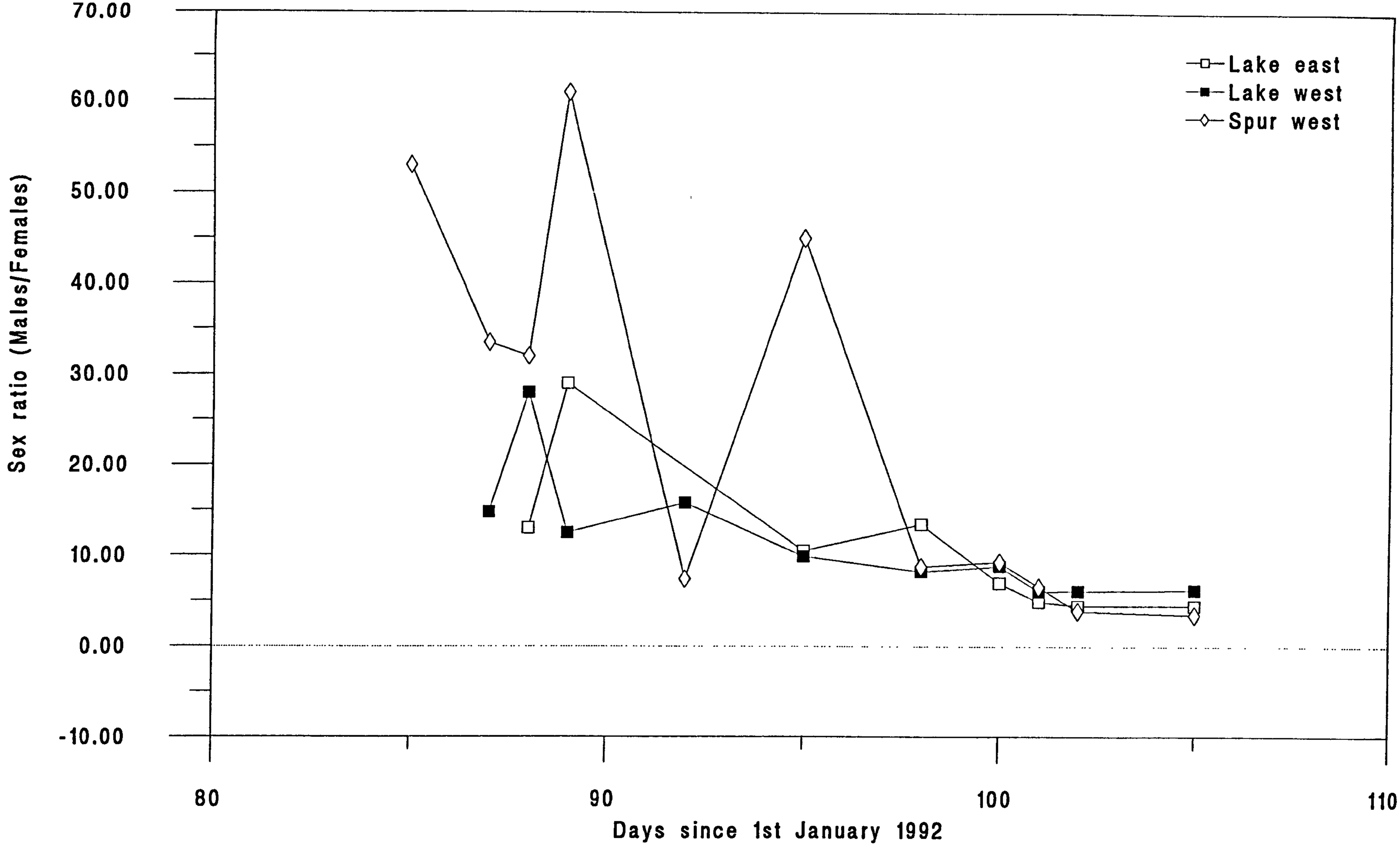


Figure 6.4: Decline in sex ratio (males:females) over the breeding season, as illustrated by data from all three banks, Osbaston Hall 1992.

TABLE 6.4: Gross catch for each drift fence and HSE as described in Table 6.1, during the three breeding seasons for the current study, Osbaston Hall.

Fence line	Code	Style	Gross catch at each trap line		
			1992	1993	1994
Spinney	SP	Drift	58	44	28
Arable West	AW	Drift	179	119	139
Arable North	AN	HSE	63	30	21
Rough Wood	REW		254	Not operational	Not operational
Rough Field	REF		233	Not operational	Not operational
Rough Inner	REI		119	Not operational	Not operational
Hedge Arable/Rough	HDI		98	114	68
Rookery (inside)	RKI	HSE	179	119	58
Rookery (outside)	RKO		54	26	17
Poplar Central (inside)	PPI	HSE	355	443	346
Poplar Central (outside)	PPO		103	101	151
Poplar North (inside)	PNI	HSE	Not operational	68	35
Poplar North (outside)	PNO		Not operational	83	28
Poplar South (inside)	PSI	HSE	Not operational	51	Not operational
Poplar South (outside)	PSO		Not operational	42	Not operational
Wood (inside)	WDI	HSE	68	Not operational	Not operational
Wood (outside)	WDO		61	Not operational	Not operational
Hedge Arable (inside) A	HAI A	HSE	Not operational	Not operational	48
Hedge Arable (outside) A	HAO A		Not operational	Not operational	31
Hedge Arable (inside) B	HAI B	HSE	Not operational	Not operational	3
Hedge Arable (outside) B	HAO B		Not operational	Not operational	3
Hedge Arable (inside) C	HAI C	HSE	Not operational	Not operational	2
Hedge Arable (outside) C	HAO C		Not operational	Not operational	6

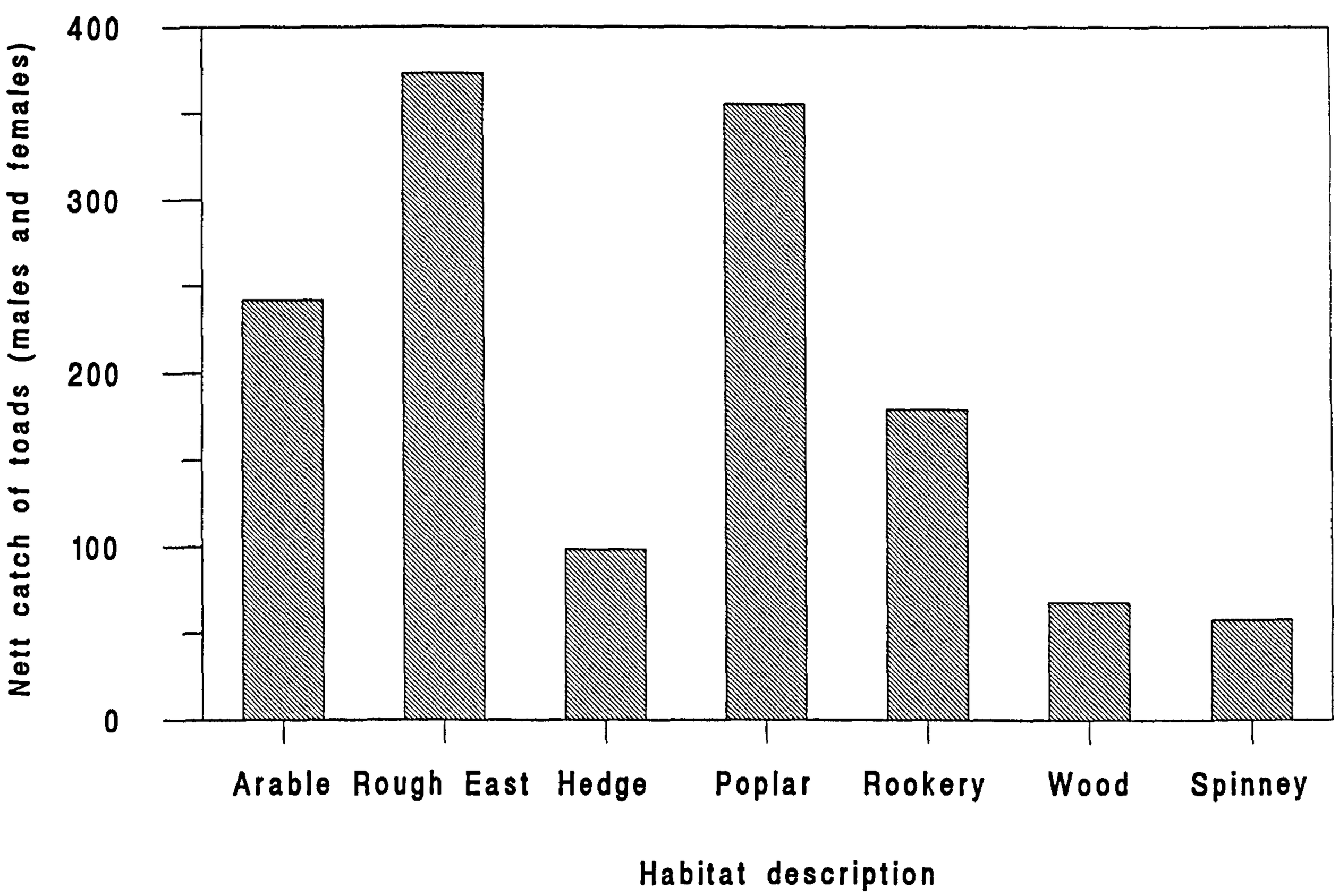


Figure 6.5: Spatial distribution of nett catch (males and females) for each of the habitats at Osbaston Hall, 1992.

Removal of the Rough East Complex traps (REW, REF, REI) almost certainly contributed to the 30% reduction in gross catch, and the proportionate increase in the toads caught in the Poplar Plantation HSE. Despite this, there were distinct changes in the spatial distribution of toads caught on site. Lower catches occurred at the Spinney (decrease of 25%) and the Rookery HSE (decrease of 34%) compared with 1992. The drift fences in the arable fields (AW, AN), provided a comparable percentage (17%) to that of 1994, but this actually represented a 34% decline in the number of toads caught.

In 1994, the gross catch was only 950, representing a decline of 25% from 1993, Table 6.4. Poplar South (PS) was discontinued, due to flooding, and the hedgerow dividing the two arable fields to the west of the breeding was fenced off into three HSE. The remaining fences remained unchanged. The spatial distribution of nett catch during the 1994 breeding influx is shown in Figure 6.7. The distribution showed similar characteristics to previous years, but the nett catch in the woodland habitats declined more than the arable habitats, for example PPI declined by 20% 1993-1994; RKI declined by 34%, and the decline observed at the Spinney in 1992-1993 continued. Despite decline at AN, the number of toads caught at AW increased, therefore the combined arable nett catch in 1994 represented 25% of the nett catch.

Gross catch over all fences declined by 44% over 1992-1994, Table 6.4. The closure of the Rough East Complex after 1992 might partly explain the decline between 1992 and 1993. However, changes in the trapping programme are unlikely to explain the 20% decline in gross catch in 1994 compared to 1993. The decline was most prominent at the SP and AN. The number of toads caught at AN fell by 65%, whilst at the SP, the number of toads caught per trap at the SP fell by 70%. The catch at RKI in 1993 was 34% down on the 1992 catch, and the 1994 catch was 50% less than the 1992 catch.

The nett catch provides an indication of the number of individuals caught at each of the drift fences, and may provide some comparison between years for each trap line. However, nett catches cannot be truly compared due to the varying 'trapping effort' between sites. Comparison of the number of toads per length of drift fence (expressed as toads/m) has been used in an attempt to 'correct' for trapping effort. The linear

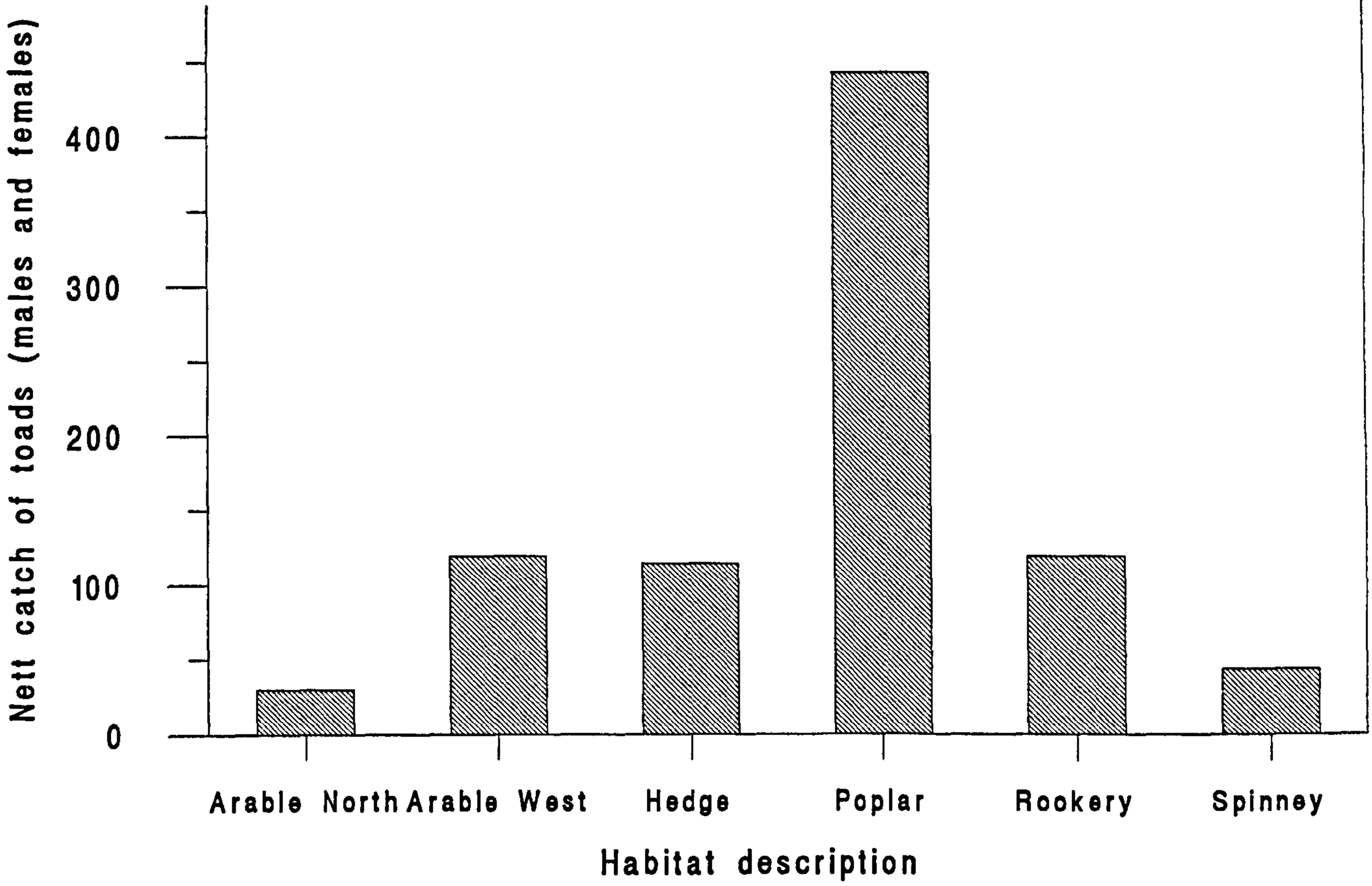


Figure 6.6: Spatial distribution of nett catch (males and females) for each of the habitats at Osbaston Hall, 1993

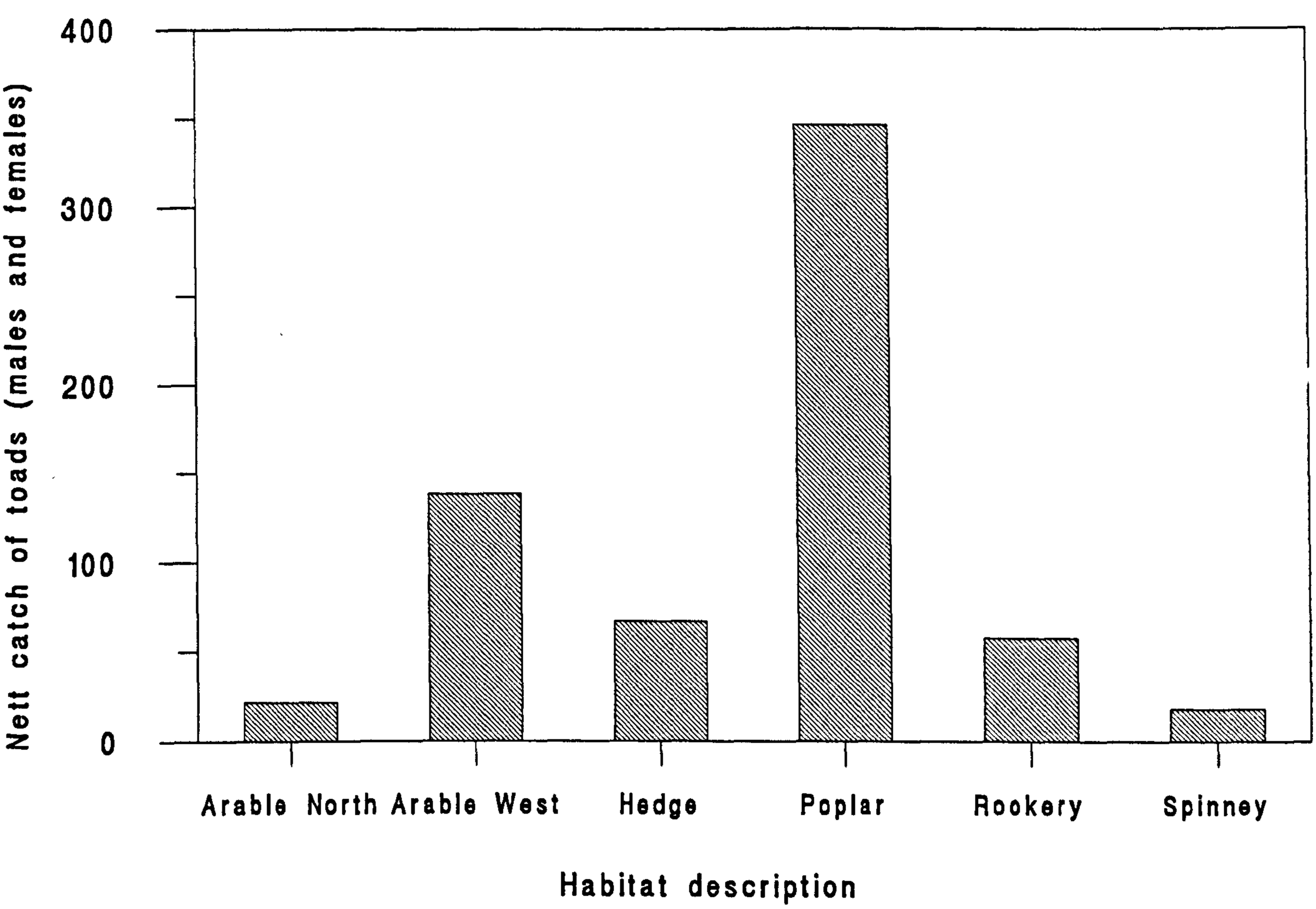


Figure 6.7: Spatial distribution of nett catch (males and females) for each of the habitats at Osbaston Hall, 1994. 128

nature of the drift fences and the fence surrounding the Wood (WDO) provides a direct calculation of catch/m. However for the circular HSEs only the outside of the fence may be used, with the diameter representing fence length rather than the actual length of chicken wire used.

The catch per metre length of fence (catch/m) at the two individual drift fences (SP, AW) was highest at Arable West (AW) for each of the four years, Table 6.5. The highest catch/m throughout the current study was seen on outside of an HSE, recorded at PNO with c. 8 toads caught/m in 1993, Table 6.5. The lowest catch/m was recorded at the Arable Hedge (HA), where all catch/m records were less than 0.5 toads/m for each section in 1994, Table 6.5. The catch/m for HDI was relatively consistent during the current study, although the catch had declined in 1994. The catch/m at SP declined over the three year study, with the greatest decline (0.44/m to 0.15/m) between 1993 and 1994. Catch/m also declined at AW; falling from 1.79 to 1.19 (1992-1993), but increasing to 1.39 in 1994. The catch/m at AN declined from 0.42/m in 1992 and to 0.20/m in 1993 and 0.14/m in 1994, Table 6.5.

The catch/m on the inside of the HSE was similar to that on the outside for the Rookery and the Wood, Table 6.5. For the Rookery, where the outside habitat was the same as that inside, this consistency might indicate that the inside catch was a fair representation of that likely throughout the habitat. The catch on the outside of the smaller circular HSEs in the Poplars (PNO, PSO) was in excess of that recorded on the inside (PNI, PSI), Table 6.5. This might indicate that the size of the circle might influence its effectiveness in capture of animals. No pattern was observed in the larger central circle in the Poplars (PPI/PPO).

Whilst the nett catches indicated a bias toward the woodland habitats (Figures 6.5 - 6.7), the catches/m were less clear (Table 6.5). Results from the Rough East Complex (1992) clearly indicated that the catch/m at fences adjacent to woodland (or hedgerow) habitat (REW and REF) were higher than those associated with the rough pasture and arable habitats (REI and AW). The catch/m at HDI was higher than that at AW in each year (bar 1992). Despite this, the catch/m at WDI in 1992 was lower than that for AN and AW, and the catch/m at the Rookery was lower than that at AW for each year.

TABLE 6.5: Catch per metre length of fence during the breeding season, Osbaston Hall. Pitfall traps were placed at a standard 10m interval from all drift fences and HSEs.

Fence line	Code	Style	Number of toads caught per metre length of fence (see Table 6.1)		
			1992	1993	1994
Spinney	SP	Drift	0.58	0.44	0.28
Arable West	AW	Drift	1.79	1.19	1.39
Arable North	AN	HSE	0.42	0.20	0.14
Rough Wood	REW		3.36	Not operational	Not operational
Rough Field	REF		2.91	Not operational	Not operational
Rough Inner	REI		1.49	Not operational	Not operational
Hedge Arable/Rough	HDI		0.33	0.38	0.23
Rookery (inside)	RKI	HSE	0.90	0.60	0.29
Rookery (outside)	RKO		0.90	0.43	0.28
Poplar Central (inside)	PPI	HSE	1.78	2.22	1.73
Poplar Central (outside)	PPO		1.72	1.68	2.51
Poplar North (inside)	PNI	HSE	Not operational	1.13	0.58
Poplar North (outside)	PNO		Not operational	8.3	2.8
Poplar South (inside)	PSI	HSE	Not operational	0.85	Not operational
Poplar South (outside)	PSO		Not operational	4.2	Not operational
Wood (inside)	WDI	HSE	0.32	Not operational	Not operational
Wood (outside)	WDO		0.29	Not operational	Not operational
Hedge Arable (inside) A	HAI A	HSE	Not operational	Not operational	0.48
Hedge Arable (outside) A	HAO A		Not operational	Not operational	0.31
Hedge Arable (inside) B	HAI B	HSE	Not operational	Not operational	0.03
Hedge Arable (outside) B	HAO B		Not operational	Not operational	0.03
Hedge Arable (inside) C	HAI C	HSE	Not operational	Not operational	0.02
Hedge Arable (outside) C	HAO C		Not operational	Not operational	0.06

6.3.1.3 Spatial distribution of catches and distance from the breeding site

The spatial distribution of catches showed a negative correlation between distance from the breeding site and the catch/m. Spearman's rank correlation provided a significant result in 1993 (r_s = -0.752, $p < 0.05$) and 1994 (rs = -0.784, $p < 0.01$), the lack of homogeneity in habitats makes this result difficult to interpret. This relationship between catch and distance from breeding site was developed at the Little Wittenham site.

The breeding site is surrounded by homogeneous stands of mature coppice and conifer plantations to a distance of around 300m, which is surrounded by sheep grazed pasture. Four circular HSEs were constructed in the deciduous woodland and three in the coniferous plantation, Figure 6.8. Each HSE was identical in construction, the only difference being its location from the breeding site. Results from Little Wittenham indicate a steady decline in the number of toads caught in the outside pitfalls over increasing distance from the breeding site for both study habitats, Tables 6.6a and 6.6b. The catches inside the HSEs did not illustrate a similar decline. Whilst in both years D1 produced the highest catch and D3 the lowest, the number of toads caught in D4 was comparable with the catch at D2. However, the catch efficiency of the HSEs at greater distance from the pond is considered to be lower, since the ratio between the area of the HSE and the sample area is higher, thus the catch in the distal HSEs would be lower than expected. A simple 'correction factor' was calculated based on the HSE:sample area ratio; providing a multiplier of 2 for C2 and D2, 3 for C3 and D3 and 4 for D4. No multiplier was used for the drift fences catches or those on the outside of the HSEs, adjusted results are provided in Table 6.6c and 6.6d. Adjusted results indicate that catches did not decline but remained consistent, or even increased with distance from the pond. Drift fences were placed on the edge of each habitat (DF and CF). Toads were caught at each drift fence, indicating that some animals had dispersed from the pond to over-winter at distances over 300m outside the woodland block, and despite the availability of favourable habitat.

6.3.1.4 Body length

In 1992, the mean length of female toads caught during the breeding migration was 64.7mm (SD = 5.2mm; N = 367; range 48 - 80mm) and mean male length was 53.7mm (SD = 3.8mm; N = 496; range 40.5 - 69.5mm), Tables 6.7a and 6.7b. There was no

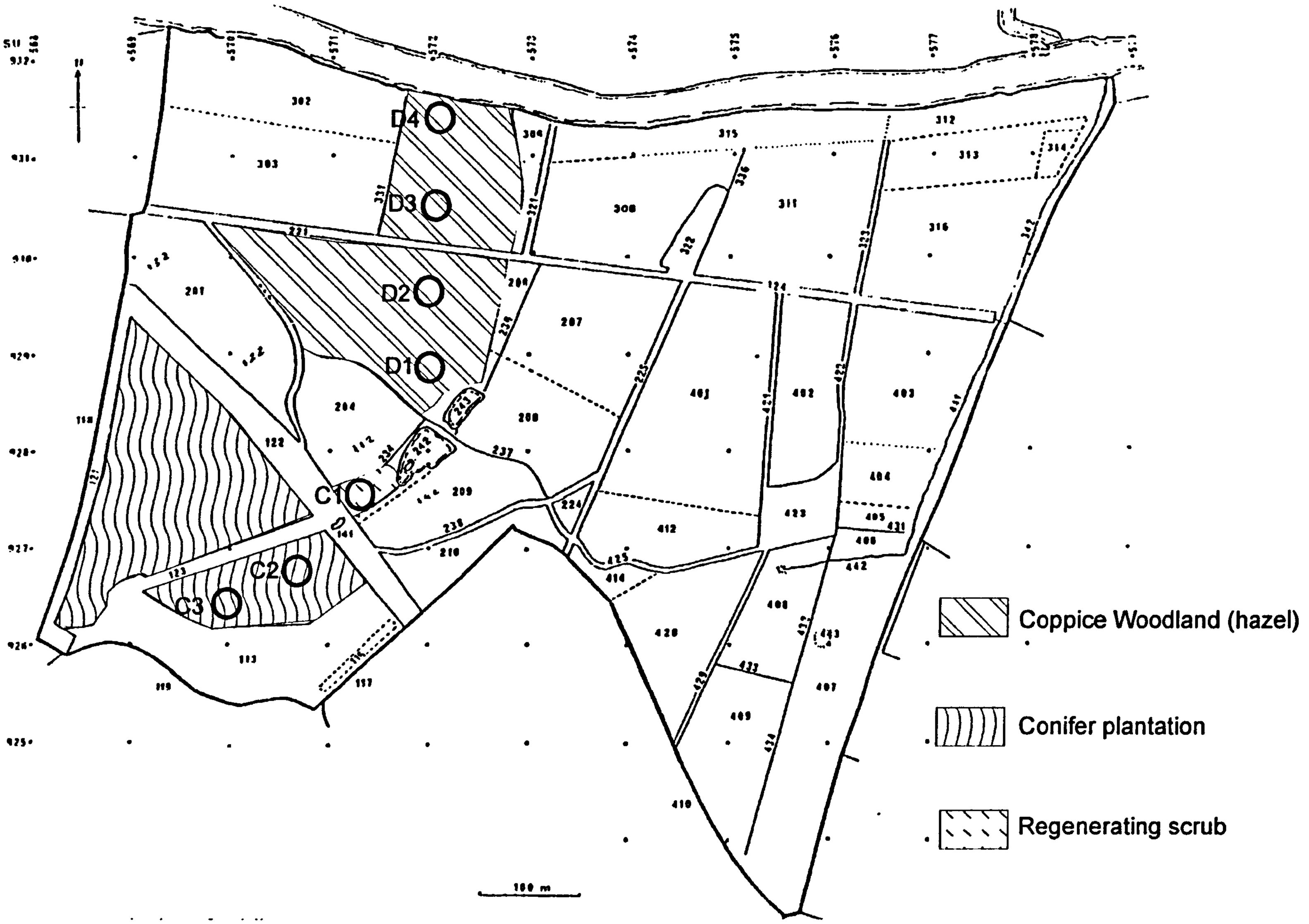


Figure 6.8: Location of Little Wittenham habitat specific enclosures (HSE) during 1994 and 1995. Note that C1, located in the regenerating scrub was not functional in 1995. Habitat types where fences were located are defined.

TABLE 6.6a: Catch number of adult toads at Little Wittenham Nature Reserve 1994. In catches are those from inside the HSE, out catches are those from the traps on the outside of the HSE. 1: Sex ratio males to females.

Habitat	Code	Catch		Sex ratio[1]	
		In	Out	In	Out
Scrub	C1	12	23	6:1	7:1
Conifer plantation	C2	1	16	1:1	2:1
Conifer plantation	C3	2	5	1:1	2:1
Conifer/grass edge	CF	N/A	15	N/A	2:1
Mature coppice	D1	17	31	1:1	2:1
Mature coppice	D2	13	15	3:1	4:1
Mature coppice	D3	2	11	*	2:1
Mature coppice	D4	8	3	1:1	2:1
Deciduous/river edge	DF	N/A	16	N/A	2:1

TABLE 6.6b: Catch at Little Wittenham Nature Reserve 1995. In catches are those from inside the HSE, out catches are those from the traps on the outside of the HSE. 1: Sex ratio males to females.

Habitat	Code	Catch		Sex ratio[1]	
		In	Out	In	Out
Scrub	C1	Not functional in 1995			
Conifer plantation	C2	2	12	2:0	3:1
Conifer plantation	C3	3	1	2:1	*
Conifer/grass edge	CF	N/A	9	N/A	1:1.3
Mature coppice	D1	12	12	3:1	2.1
Mature coppice	D2	6	24	2.3:1	6.7:1
Mature coppice	D3	1	4	*	1:1
Mature coppice	D4	6	1	1:1	*
Deciduous/river edge	DF	N/A	6	N/A	1:1

TABLE 6.6c: Catches (raw and adjusted) for coniferous (C1-C3) and deciduous habitats (D1-D4) at Little Wittenham Nature Reserve 1994. 1: Estimated through the geometric relationship between the size of the enclosure and sample area. 2: Adjusted catch multiplied by the correction factor.

Fence	Distance from pond	Correction factor[1]	Catch (inside HSE)	
			Raw	Adjusted[2]
C1	75	1	12	12
C2	150	2	1	2
C3	225	3	2	6
D1	75	1	17	17
D2	150	2	13	16
D3	225	3	2	6
D4	300	4	8	32

TABLE 6.6d: Catches (raw and adjusted) for coniferous (C1-C3) and deciduous habitats (D1-D4) at Little Wittenham Nature Reserve 1994. 1: Estimated through the geometric relationship between the size of the enclosure and sample area. 2: Adjusted catch multiplied by the correction factor.

Fence	Distance from pond	Correction factor[1]	Catch (inside HSE)	
			Raw	Adjusted[2]
C1	Not functional			
C2	150	2	2	4
C3	225	3	3	9
D1	75	1	12	12
D2	150	2	6	12
D3	225	3	1	4
D4	300	4	6	24

TABLE 6.7a: Mean (with standard error) and median lengths (mm) for female adult toads, Osbaston Hall. Recaptures during the same year are not included in the data set. For key for habitat codes see Table 6.1.

Habitat	1992		1993		1994	
	Mean	Median	Mean	Median	Mean	Median
AN	65.1 ± 0.9	67.3	66.1 ± 1.1	66.0	64.3 ± 1.0	65.5
AW	64.6 ± 0.9	65.3	64.3 ± 1.7	64.3	67.4 ± 0.8	67.8
SP	66.5 ± 0.8	66.0	61.5 ± 3.4	66.0	68.6 ± 1.4	67.0
PPI	62.4 ± 1.1	62.0	63.0 ± 1.9	63.5	65.3 ± 0.8	66.0
RKI	66.4 ± 0.9	66.3	62.9 ± 0.8	62.0	64.3 ± 1.6	64.3
HW	64.3 ± 0.9	65.5	63.4 ± 1.6	66.0	64.4 ± 2.4	66.0
WDI	64.8 ± 1.2	64.5	Not functional			
REI	65.3 ± 1.2	65.7				
REF	65.9 ± 1.7	62.5				
REW	63.9 ± 0.5	64.0				

TABLE 6.7b: Mean (with standard error) and median lengths (mm) for male adult toads, Osbaston Hall. Recaptures during the same year are not included in the data set. For key for habitat codes see Table 6.1.

Habitat	1992		1993		1994	
	Mean	Median	Mean	Median	Mean	Median
AN	55.7 ± 1.12	54.5	58.3 ± 1.09	57.6	54.5 ± 1.5	54.5
AW	52.8 ± 0.58	52.5	53.5 ± 1.61	53.5	52.7 ± 1.14	52.0
SP	56.2 ± 0.82	57.0	53.1 ± 4.19	56.3	55.7 ± 2.32	56.0
PPI	52.9 ± 0.53	52.5	51.8 ± 1.70	50.0	53.7 ± 0.46	53.5
RKI	53.5 ± 0.39	53.5	56.5 ± 0.86	56.5	55.0 ± 0.46	55.0
HW	54.5 ± 0.35	54.5	55.9 ± 1.86	56.3	52.0 ± 2.50	54.5
WDI	53.8 ± 0.85	53.5	Not functional			
REI	52.8 ± 0.72	52.2				
REF	53.0 ± 0.66	53.0				
REW	54.5 ± 0.49	54.0				

TABLE 6.7c: Inter-year variation in total catch, trapping period, peak migration mean mass, mean length and over sex ratio, 1992-1994, Osbaston Hall. 1: Condition sensu Kuhn 1994. Mean masses calculated for all toads (except those recaptured within the same year).

Year	Total catch	Mean condition[1]		Mean mass[2]		Mean length[2]		Sex ratio
		Males	Females	Males	Females	Males	Females	
1992	1726	111.2	123.9	17.4	34.2	53.7	64.8	4.4:1
1993	1249	111.6	131.2	19.1	38.6	55.3	66.0	3.8:1
1994	969	112.3	129.0	18.9	38.1	54.1	66.2	2.9:1

significant difference in female length from each of the catch habitats (ANOVA, F = 1.50; p = 0.147), although those females caught within the Rough East enclosure (REI) appeared slightly smaller than the other habitats, Table 6.7a. The mean length for male toads caught in each habitat was significantly different (ANOVA, F = 2.41; p < 0.05), 6.7b. The Tukey test (for unplanned multiple comparison) was used to establish where the variation occurred within the ANOVA calculation. Thirty-nine of the 45 comparisons where greater than the critical value of 4.47. The largest animals were caught at the traps the furthest from the breeding site at SP and AN, and significantly larger than the smallest animals caught in PPI, Table 6.7b. Tables showing Tukey test results are provided in Appendix 7.

In 1993, the mean length of female toads caught during the breeding migration was 65.6mm (SD = 5.6mm; N = 131; range 52.5 - 85mm), and 54.9mm (SD = 4.5mm; N = 83; range 44 - 68mm) for male adult toads, Table 6.7a and 6.7b. There was no significant difference between the lengths of the females from each of the catch habitats (ANOVA, F = 0.74, p = 0.74), although those caught at the AN appeared slightly larger than the animals from the remaining habitats. The mean length of the males caught from the different habitats was not significantly different (ANOVA, F = 1.21; p = 0.318), Table 6.7b.

In 1994, the mean length of female toads caught during the breeding migration was 65.9mm (SD = 5.4mm; N = 216; range 28 - 78mm) and was 54.3mm (SD = 3.9mm; N = 227; range 44 - 65mm) for males, Table 6.7a and 6.7b. Although those females caught at the AN again appeared slightly larger than the animals from other habitats, there was no significant difference between the lengths of the females from each of the habitats (ANOVA, F= 1.29, p = 0.271, N = 125), Table 6.7a. There was no significant difference in the length of the males from each of the habitats (ANOVA, F = 1.12, p = 0.350, N = 146), Table 6.7b.

The mean length of both the males and females remained consistent over the three years 1992-1994, Tables 6.7a, 6.7b and 6.7c. There was some variation in the size distribution of females arriving at the breeding pond, Figure 6.9, although there was a decline in the number of both larger males and smaller males in 1994, Figure 6.10.

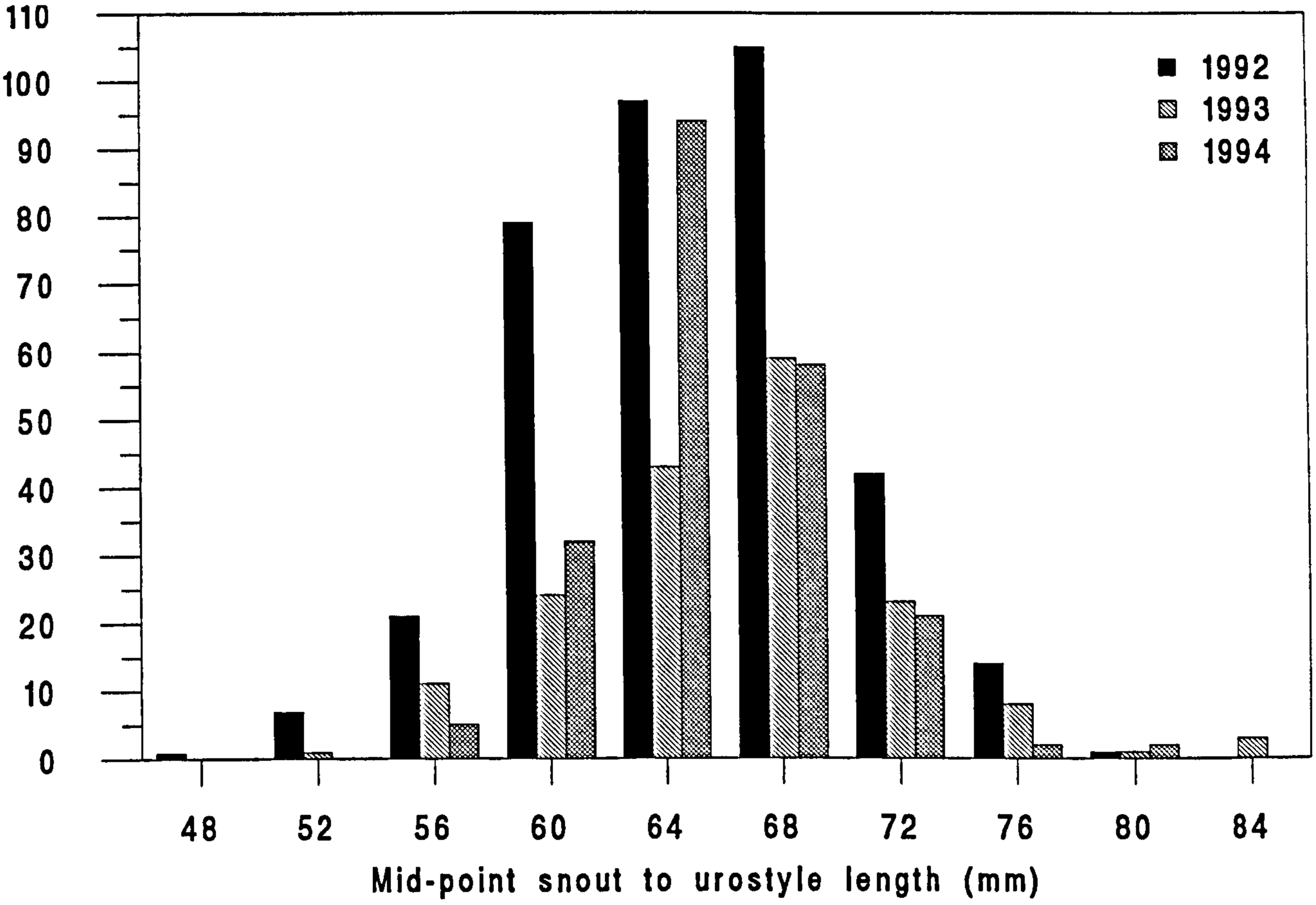


Figure 6.9: Length frequency of female toads caught during the breeding season 1992-1994.

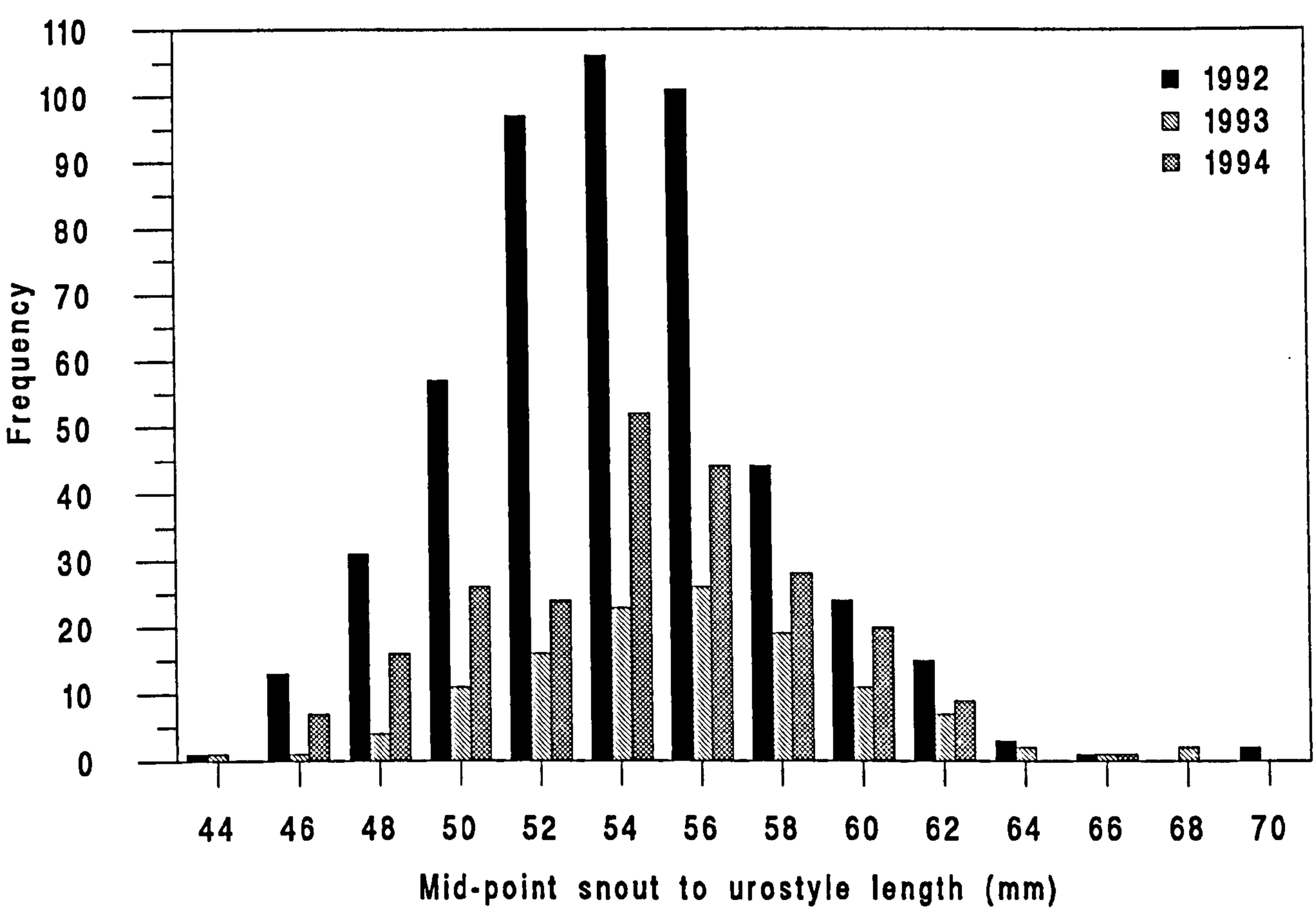


Figure 6.10: Length frequency of male toads caught during the breeding seasons 1992-1994.

A lack in variation in the length of adults coming from different habitats might suggest that a minimum length is required prior at breeding, this may be especially important if survival limits an animal to only one year's breeding.

Daily catches at the pitfall traps over the course of the 1992 and 1994 breeding seasons showed that the mean length of the male toads migration declined over the migration, with the largest individuals migrating earliest. In 1992, the males arriving after the main inward migration were 6% smaller than males arriving at the start of the migration. The decline was more clearly shown after the mean length for each catch day was smoothed using a five-point moving average, Figure 6.11. There was a significant correlation between day and length for males ($r_s = -0.793$, $n = 15$). A similar trend was evident for the females in 1992 ($r_s = -0.907$, $n = 12$), Figure 6.12. In 1994, the mean length of the males caught on successive days during the breeding season declined over the first half of the season, but then increased over the latter part.

6.3.1.5 Individual toad condition

In 1992, there was no significant difference in the condition[1] (ANOVA, $F = 1.04$; $p = 0.410$; $N = 312$) of females originating from each habitat during the breeding season, Table 6.8a. Male condition was significantly different (ANOVA, $F = 2.81$; $p < 0.01$; $N = 412$), Table 6.8b. The Tukey test was again used to establish where the variation occurred within the ANOVA calculation. Thirty-two of the 45 comparisons where greater than the critical value of 4.47. Male toads in better condition generated from the Rough East Complex and those in poorer condition from RKI, the SP and the HDI. Interestingly, there was no significant variation between the samples originating from the arable habitats (AW and AN). Tables showing Tukey test results are provided in Appendix 7.

As in 1992, for 1993 there was no significant difference in the body condition of females caught in each of the habitats (ANOVA, $F = 1.70$; $p = 0.410$; $N = 120$), Table 6.8a, but a significant difference in condition for the males (ANOVA, $F = 2.77$; $p < 0.01$; $N = 55$), Table 6.8b. Male toads in highest condition were caught at Arable North and those in

[1] The condition index was normalised using a log transformation prior to analysis.

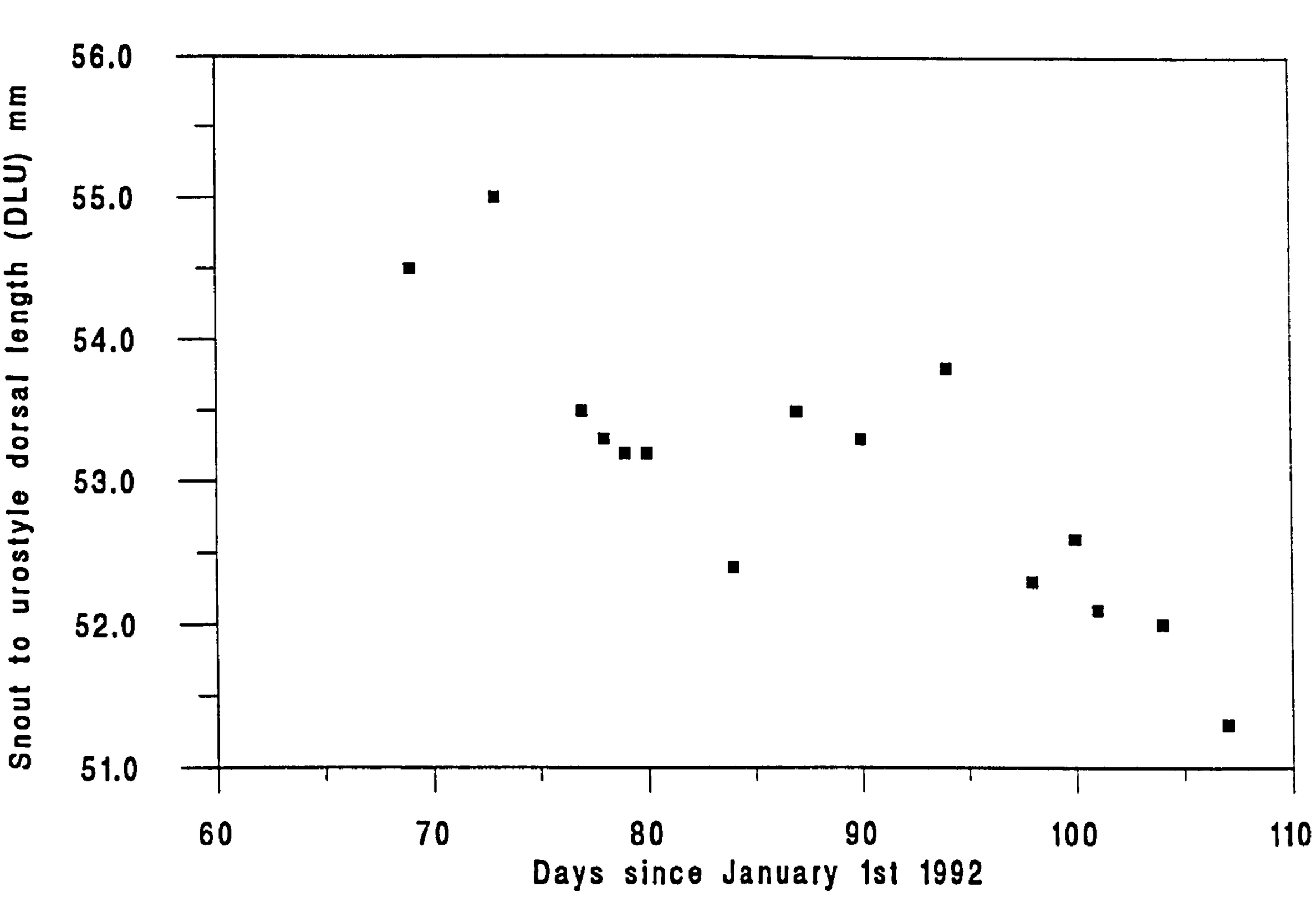


Figure 6.11: Decline in the length (DLU) of male toads caught during the 1992 breeding season. The slope has been smoothed using a five-point moving average.

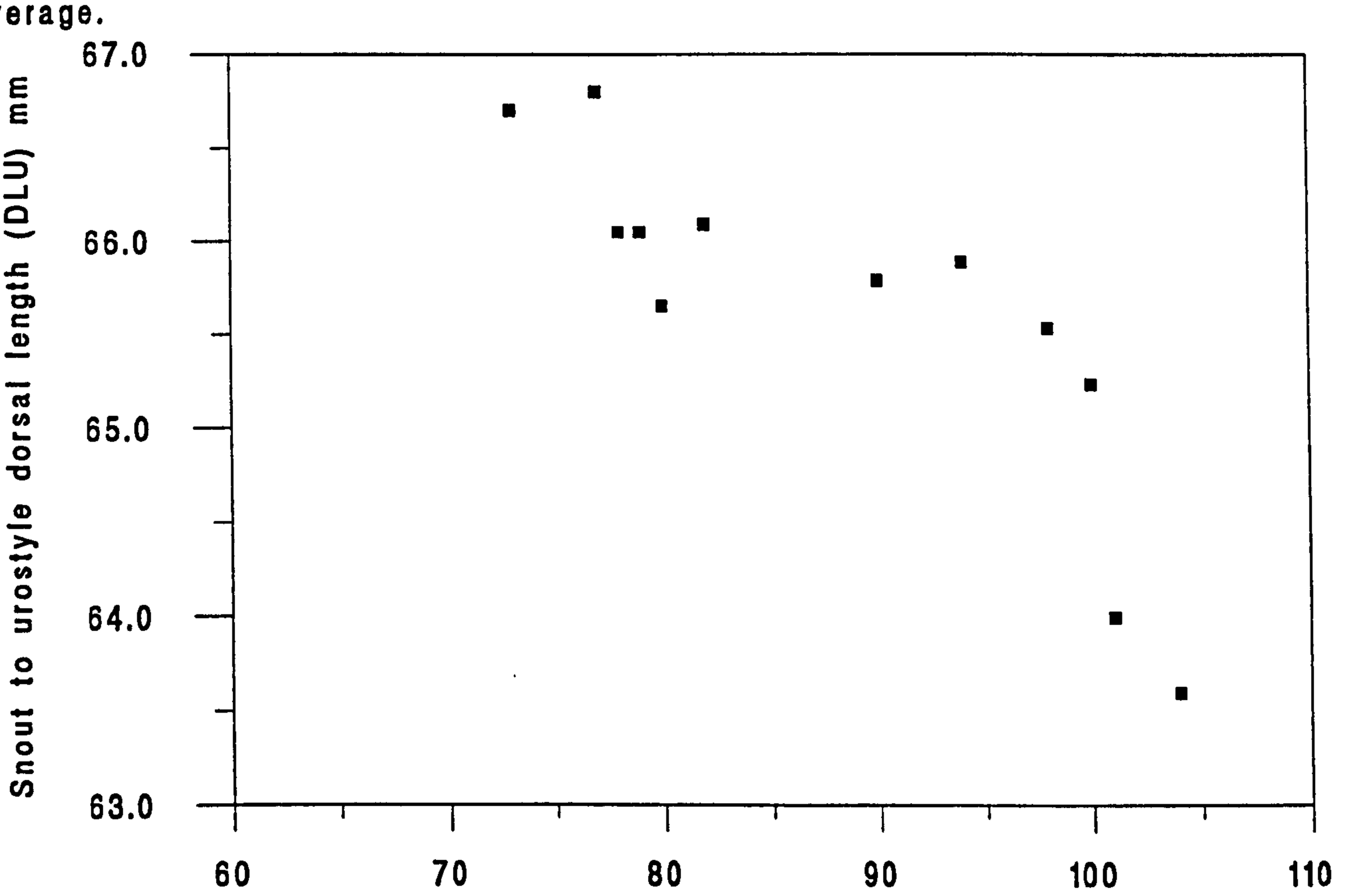


Figure 6.12: Decline in the length (DLU) of female toads caught during the 1992 breeding season. The slope has been smoothed using a five-point moving average.

TABLE 6.8a: Mean (with standard error) and median condition (using Kuhn 1994) for female adult toads, Osbaston Hall. Recaptures during the same year are not included in the data set. For key for habitat codes see Table 6.1.

Habitat	1992		1993		1994	
	Mean	Median	Mean	Median	Mean	Median
AN	123.21 ± 1.8	123.7	129.8 ± 2.3	131.2	122.5 ± 2.8	126.7
AW	126.40 ± 1.7	126.4	123.8 ± 4.2	128.0	129.4 ± 1.8	128.8
SP	122.94 ± 2.4	122.5	128.6 ± 4.0	131.1	130.1 ± 3.2	129.7
PPI	124.74 ± 2.0	124.8	123.5 ± 3.6	124.1	122.5 ± 2.8	123.1
RKI	121.15 ± 1.9	119.8	127.1 ± 2.9	125.7	150.5 ± 30.6	122.2
HW	118.61 ± 1.9	119.6	133.4 ± 2.3	134.3	197.4 ± 63.6	130.8
WDI	123.86 ± 3.6	120.7	Not functional			
REI	123.54 ± 2.0	123.1				
REF	120.25 ± 3.2	119.9				
REW	124.20 ± 1.4	124.3				

TABLE 6.8b: Mean (with standard error) and median condition (using Kuhn 1994) for male adult toads, Osbaston Hall. Recaptures during the same year are not included in the data set. For key for habitat codes see Table 6.1.

Habitat	1992		1993		1994	
	Mean	Median	Mean	Median	Mean	Median
AN	111.30 ± 3.13	112.37	125.6 ± 8.11	132.8	116.4 ± 3.12	116.44
AW	112.39 ± 1.62	111.14	105.5 ± 1.54	105.5	115.5 ± 2.15	113.83
SP	107.34 ± 2.34	105.34	116.3 ± 5.07	115.9	121.4 ± 1.32	121.3
PPI	115.37 ± 1.69	112.37	114.2 ± 2.93	113.9	112.8 ± 1.01	111.95
RKI	111.01 ± 0.99	111.03	107.3 ± 2.13	106.9	109.7 ± 1.69	109.3
HW	107.52 ± 1.08	107.10	118.2 ± 3.13	116.8	116.9 ± 5.41	116.9
WDI	108.72 ± 2.65	108.89	Not functional			
REI	114.08 ± 2.02	111.54				
REF	115.67 ± 2.78	120.19				
REW	110.22 ± 1.28	108.81				

poorer condition generated the Rookery (RKI) and Arable West (AW). Tables showing Tukey test results are provided in Appendix 7.

Again, in 1994 there was no significant difference in the condition of female toads caught from each of the habitats during the breeding season (ANOVA, F = 0.99; p = 0.426; N = 125), Table 6.8a. Unlike 1992 and 1993, in 1994 there was no significant difference in the condition of males catch in each of the habitats (ANOVA, F= 1.79; P = 0.129; N = 120), Table 6.8b.

Over the three years of study mean male condition over the nett catch varied little, whilst the condition of females in 1992 appeared poorer than for females in subsequent years. Consistency in the condition of females generating from different habitats may indicate a minimum condition required for breeding. The fact that males from certain habitats (RKI and PPI) were in poorer condition that males from other habitats (Rough East Complex) might suggest that condition is less important in determining the breeding viability of male.

6.3.1.6 Sex ratio

The gross catch at Osbaston was biased towards males in each year of the current study, Table 6.9. Although the ratio fell from 4.4:1 (1992) to 2.9:1 (1994), representing an observed decline over the current study, there was a consistent spatial pattern in the sex ratio from the catches for each of the traplines with high sex ratio observed in the enclosures closest to the ponds, notably the PPI, and the low sex ratio (indeed female dominance) at the more distal catch sites (Spinney). The sex ratio was observed to be in favour of females for the catch at the Arable North fence in 1993 and 1994 and for the Spinney in 1994.

The overall sex ratio for each habitat was highest for the woodland catches; Wood (1991-92 only), RKI, PPI and SP and lowest for the fences in the two arable fields (AW and AN), Table 6.10. The overall sex ratio for the pasture habitat (1992 only) was 3.5:1. Given the overall decline in the sex ratio of the gross catch over the current study, the woodland catch showed a distinct decline; 7.2:1 in 1992 compared with 3.8:1 in 1994. The sex ratio from the arable catch remained consistent (2:1).

TABLE 6.9: Sex ratio in habitats at Osbaston. Where data are presented from an enclosure the ratio represents the catch from inside (see Table 6.1).

Habitat	Distance from pond (m)	Sex ratio (M:F) observed in catch		
		1992	1993	1994
PPI	25	12.2:1	8.2:1	2.3:1
AW	100	2.5:1	4:1	2.5:1
HA	> 100	not functional		1.7:1
REI	160	4.8:1	not functional	
WDI	175	2.6:1	not functional	
HW	200	2.8:1	2.3:1	2:1
AN	210	1.1:1	1:5	1:3.2
RKI	250	8:1	2.4:1	3.4:1
SP	400	1.8:1	1:1	1:3.5
Overall		4.4:1	3.8:1	2.9:1

TABLE 6.10: Simplified sex ratio in grouped habitats types at Osbaston. Where data are presented from an enclosure the ratio represents the catch from inside (see Appendix for fence descriptions).

	Sex ratio (M:F) observed in catch		
Habitat	1992	1993	1994
Wood	7.2:1	5.2:1	3.8:1
Pasture	3.5:1	not functional	
Arable	2:1	2:1	1.9:1
% Female	20	21	29

The percentage of females in the gross catch was consistent in 1992 and 1993 at 20% but rose to 30% in 1994; when linked to the fall in gross catch in 1994, this suggests a fall in the male population during 1993-94.

6.3.1.7 Evaluation of the adult monitoring methodology

6.3.1.7.1 Drift Fences

The toad fences used throughout the current study were estimated to be 58-65% efficient in capturing toads that encountered the fence, Table 6.11. The construction of the fences with the additional 'T' did not appear to increase efficiency, suggesting that the number of animals climbing over the fence was limited. Those animals that evaded capture from the basic design are assumed to have done so, therefore, by exploiting gaps in the fence, although small males have the ability to push themselves through the chicken wire mesh. Covering the chicken wire with polythene sheeting increased the efficiency of the fences to nearly 90%. This design was used at Little Wittenham in 1994 and 1995 and in the northern circle at Osbaston.

6.3.1.7.1 Night counts

Completion of a mark, release and recapture exercise (MRR) during the peak of the breeding season (Osbaston 1992, 1993, LWNR 1995) provided an estimate of the total breeding male population (with an associated error) and the opportunity to evaluate the efficiency of the use of the peak night count in assessing population size. During 1992 the MRR exercise was completed during a declining population, conversely the 1993 exercise was completed whilst the population was still rising. At Little Wittenham the night-counts illustrated that the exercise probably caught the breeding peak.

At Osbaston, the peak night count accounted for 25% of the estimate for the adult population provided by the MRR, Tables 6.12a-6.12b. At Little Wittenham, peak night count obtained on circuits of the entire lake amounted to only 10% of the estimated breeding male population for that year, Table 6.13. Counts obtained at Llandrindod Lake, for a total population of 8000 (Gittins, Parker and Slater 1980) and at a newly established site in Peterborough with a population of 3-6000 recorded less than 5% of that population estimate. Without the MRR, these figures would be impossible to

TABLE 6.11: Efficiency of bare chicken wire (poplar central) compared to the fence covered in polythene sheeting (poplar north), Osbaston Hall Estate, 1994 with data from Little Wittenham for comparison 1994, 1995. 1: Catch rate represents the number of toads caught in proportion to fence length (m). 2: Fence efficiency is the % of marked released toads recaptured in the pitfalls.

	Area	Catch rate [1]	Efficiency (Fe)[2]
Poplar central - 1993	c. 2000m^2	2.24	64%
Poplar central - 1994	c. 2000m^2	1.84	58%
Poplar north - 'T' design	c. 450m^2	1.36	50%
Poplar north - sheeting	c. 450m^2	0.54	82%
Wittenham 1994	c. 200m^2	0.3	85-89%
Wittenham 1995	c. 200m^2	0.2	88-90%

TABLE 6.12a: Male breeding population estimate, Osbaston Hall 1992. 1: Population size estimated by Jolly's method, bar day 1 when Jolly's does not apply and Lincoln is used. 2: The total number of males (single males + paired males) counted in the water body. The timing of the exercise is provided by the day of the year in parenthesis.

	Day 1 (99)	Day 2 (101)	Day 3 (103)
Estimate [1]	2950 ± 530	1675 ± 765	N/A
Count [2]	918	688	360
%	26 - 38 %	28 - 76 %	N/A

TABLE 6.12b: Male breeding population estimate, Osbaston Hall 1993. 1: Population size estimated by Jolly's method, bar day 1 when Jolly's does not apply and Lincoln is used. 2: The total number of males (single males + paired males) counted in the water body. The timing of the exercise is provided by the day of the year in parenthesis.

	Day 1 (78)	Day 2 (80)	Day 3 (82)
Estimate [1]	612 ± 48	1187 ± 208	N/A
Count [2]	202	617	695
%	30 - 35 %	48 - 63 %	N/A

TABLE 6.13: Male breeding population estimate, Little Wittenham Nature Reserve 1995. 1: Population size estimated by Jolly's method, bar day 1 when Jolly's does not apply and Lincoln is used. 2: The total number of males (single males + paired males) counted in the water body. The timing of the exercise is provided by the day of the year in parenthesis.

	Day 1 (83)	Day 2 (85)	Day 3 (87)	Day 4 (89)	Day 5 (91)	Day 6 (93)	Day 7 (93)
Estimate [1]	3312 ± 1445	2341 ± 1108	600 ± 143	2868 ± 863	1999 ± 588	1752 ± 751	N/A
Count [2]	183	214	170	265	403	233	120
	4 - 10 %	6 - 17 %	23 - 37 %	7 - 13 %	16 - 29 %	9 -23 %	N/A

calculate.

Variation in the success of head counts may be attributed to the morphology of the pond; a small pond is likely to support a smaller population than a larger pond, but peak counts may reveal a higher percentage of the population, purely on the grounds of the ease of visibility. Ponds where visibility is reduced, through the turbidity of the water, or through emergent vegetation, will suffer from a reduction in the efficiency of the head counts. Males remain in the water for longer periods than females, whilst the MRR exercise removes the possibility of double counting, due to the unique marking system, this is not possible using only a head count. It might, therefore, be that males are over-represented using head counts only, whilst females, who are less conspicuous and leave the pond soon after spawning, may be under-represented. During high head counts (in excess of 400 animals) double counting becomes more of a probably due to the extended time to count the visible animals. When temperatures fall below 4-6 °C, activity is reduced and night counts do not reflect the number of toads in the water, see Day 3, LWNR Table 6.13.

These difficulties will be site specific, therefore whilst head counts are valuable in determining presence of a toads and suggesting abundance, comparison of head counts from pond to pond is invalid without an assessment of the accuracy of the night count for each and every pond.

6.3.2 Metamorph output 1991-1994

The temporal pattern of captures at the traps was characterised by a peak, during which about 30% of the gross metamorph catch occurred. The temporal pattern for the catch from the Lake is shown in Figure 6.13. The spatial pattern of catches from the Lake during 1991-1993 showed a distinct move towards emergence on the western side; in 1991, 85% of the gross metamorph catch of metamorphs left the Lake by its western bank, in 1993, 95% of the catch occurred on the western bank. A marked decline in the number of metamorphs occurred on both the northern and eastern banks over the years 1992-1994, Table 6.14.

Total emergence over 1991-1994 was highly variable, although the emergence (in

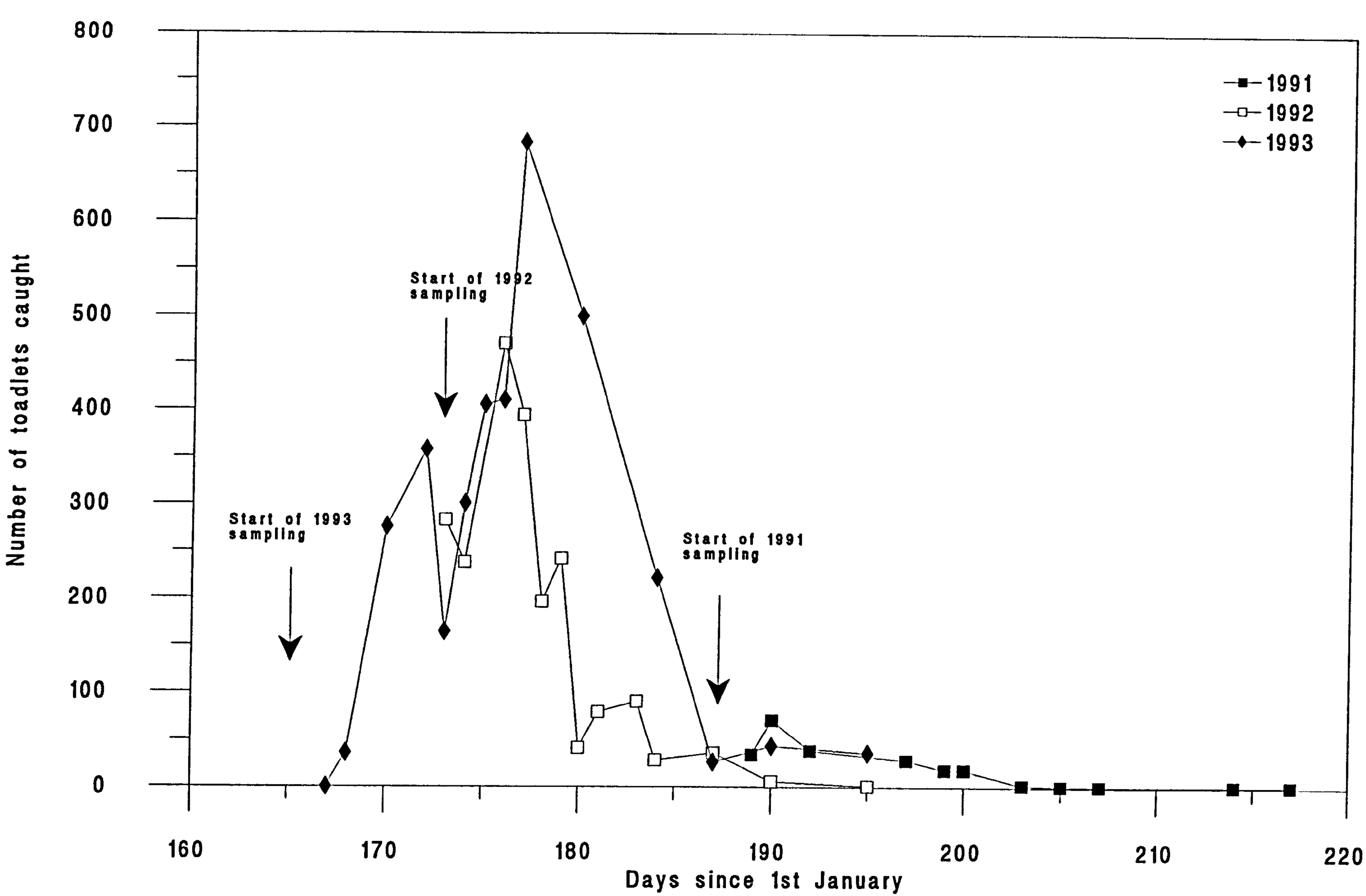


Figure 6.13: Temporal pattern of toadlet emergence at the lake, Osbaston Hall during 1991-1993

TABLE 6.14: Pattern of metamorph emergence from the Lake, Osbaston 1991-1994. Output shown as total emergence.

Year	Emergence	Percentage emerging from each side			
		North	East	South	West
1991	c 14,000	10.4	3.5	1.5	85.1
1992	c 136,000	8.6	9.5	1.2	80.5
1993	c 220,000	1.4	1.1	1.7	95.8
1994	< 2,000	In appropriate sample size			

TABLE 6.15: Output of metamorphs from the Lake, Osbaston1991-1994. Output shown as total emergence.

Year	Estimated emergence from each side				
	Total	North	East	South	West
1991	14,000 ± 170	c. 1,400	c. 500	c. 200	c. 12,000
1992	136,000 ± 4,000	11, 500 ± 1,360	13, 650 ± 850	2,310 ± 350	110,500 ± 5,200
1993	220,000 ± 10,000	7,300 ± 1,000	2, 450 ± 200	3,010 ± 710	215,000 ± 15,300
1994	< 2000	Inappropriate sample size			

number and per metre) from the Spur was consistently lower than the Lake. The highest output from the Spur (4000 ± 170, 1992) represented less than 5% of the comparative Lake output. This represented a density of 15 metamorphs/m around the Spur compared to a density of 380 ± 10 metamorphs/m around the Lake. The output from the Lake increased during 1991-1993. In 1991, an estimated 14,000 ± 170 (202 animals caught) emerged from the lake. This increased to 136,000 ± 4000 in 1992, and to 220,000 ± 10,000 in 1993, but in 1994 there was a emergence failure, Table 6.15.

6.4 Discussion

6.4.1 Spatial distribution and variation in gross catch 1992-94

The woodland habitats (particularly PPI), or habitats adjacent to woodland (REW) provided the highest proportion of the catch, and this was a consistent feature from year to year. Gross catch from the woodland habitats outnumbered catches from the arable areas (Arable West, Arable North) by a factor of 3.45, Table 6.4. Nett catches also showed a bias toward woodland habitats, Figures 6.5-6.7.

Data from previous studies indicate that a higher number of toads are observed within habitats including areas of woodland than reported in arable habitats (Honjanina 1953, Karg and Mazur 1969, Oldham and Swan 1991, Salvidio, Cresta and Dolmen 1993). Toad catches from the Habitat Specific Enclosures (HSE) at Little Wittenham located in deciduous woodland outnumbered those in coniferous woodland, at equal distances from the breeding site, by a factor of two, Table 6.6a and 6.6b. Similar results are available for other anuran species, namely the common frog (*Rana temporaria*) where catches in deciduous forests (Glowacinski and Witkowski 1970) were over twice those observed in coniferous forests (Inozemtsev 1969). Therefore, it appears that woodland vegetation may be considered to be an important habitat feature for the toad and anurans in general, by providing shelter from predation and desiccation and may also be more beneficial in terms of food availability (Cornish 1993).

6.4.2 Body length, mass and condition

The length of males or females from the various habitats did not vary significantly (with the exception of male length in 1992). This may indicate that a minimum length is required to be obtained by males and females for breeding to be viable.

Males caught in the Rookery HSE (RKI) were in a significantly poorer condition than other males in both 1992 and 1993, notably those from the east of the breeding site (REI, REF and AN). This pattern continued in 1994, but was not statistically significant. In contrast, females did not illustrate any significant pattern of body condition that could be linked to habitat. This was in contrast to the original hypothesis; that female condition would provide a valuable indication of habitat quality. Condition is a reflection

of mass and length and therefore may be used to estimate the health of the individual and therefore indicate the availability of resources over the previous season. Females under resource pressure may abandon egg production to ensure that they achieve a level of body condition that will ensure survival over the winter. Females in poor condition are unlikely to survive the winter and those with no eggs may not breed. The catch during the breeding season may therefore represent only those females that have a history of sufficient resources to provide both energy for egg production and good body condition. Given this assumption, the condition necessary for breeding in females is unlikely to vary between habitats and no difference would be observed.

Gittins (1993a) suggested that those females that did not hold sufficient eggs, at the onset of the breeding season, for breeding to be viable, might not breed that year; breeding being postponed for a year (or more) until the female could accumulate sufficient resources for egg production. The apparent lack of a significant difference in female condition between habitats could be viewed in a similar fashion. Males might not, however, be restricted by condition at breeding, as the energy requirements for sperm production are likely to be less than for egg production. Once sexual maturity has been achieved in males (as indicated by length), it appears that males of various conditions may breed. Since males appear to breed regardless of inferior body condition they should be considered as more opportunistic in their breeding behaviour.

The body lengths of the females from Osbaston Hall were between 20-22% longer than the males. This size difference in the current study is smaller than the figures quoted by Gittins *et al.* (1980), 23.6% and 25.5% in Mid-Wales; and by Reading (1990), 24.3% and 27.9% in Dorest; although larger than the 16% quoted by Reading (1990) for common toads in southern Spain. The difference between the length of adult females and males at Little Wittenham, Oxfordshire was only 15.8%, Table 6.16. A larger size is beneficial for the female in breeding and fecundity. Females are believed to reach breeding maturity at least one year after males (Gittins 1983a). The difference between the sizes of adult females and males, in part, reflects the difference in the time required for each sex to reach adulthood. There is limited data available on the comparative growth rates between males and females during the sub-adult stage, although it is known that growth rates slow once adult status is reached (Chapter 8). It may however

TABLE 6.16: Comparison in the variation in male and female lengths from available literature.

Reference	Study area	Mean SVL (mm)		Difference (%)
		Males	Females	
Gittins *et al.* 1980	Mid-Wales	N/A	N/A	23.6
Gittins *et al.* 1980	Mid-Wales	N/A	N/A	25.5
Reading 1990	Purbeck, Dorest	68	86-97	27.9
	Portland, Dorest	61	77	24.3
cited in Reading 1990	Spain	N/A	N/A	16.0
Salvidio *et al.* 1993	Central Norway	63	73	15.8
Oldham 1985	NW Leicestershire	53	65	22.6
Oldham 1985	NW Leicestershire	56	68	21.4
Latham *et al.* 1994	Oxfordshire	57	66	15.8
This study 1992	NW Leicestershire	54	65	20.4
This study 1993	NW Leicestershire	53	66	20.0
This study 1994	NW Leicestershire	54	66	22.2

be assumed that growth rate is comparable between males and females during the sub-adult stage. In the year males reach maturity their annual growth reduces, whilst the females' growth will continue at the sub-adult rate until it too reaches adult status. Common toads in southern Spain have a longer foraging period, due to the warmer climate, therefore both males and females may achieve adult status in a shorter period than those in the UK. Perhaps the high quality of habitats available at Little Wittenham may explain the variation in the size of males and female adults where resources allow earlier maturing.

Toads under resource pressure due to population density, or poor quality terrestrial habitat may require longer period to reach maturity and therefore the size difference between the sexes is increased, in order to develop this hypothesis there needs to be an understanding of the age of the toads reaching adult status and this is discussed in Chapter 8.

6.4.3 Changes in size distribution in the breeding populations during different years

The decline in the proportion of smaller females in the 1994 catch compared with the 1992 catch, might suggest that there was a reduction in younger animals in the adult population, Figures 6.9 and 6.10. During the juvenile and adult stage up to first breeding the relationship between age and length is considered linear. This decline might be a reflection of higher mortality during the juvenile stage, given an equal number of individuals entering the population, or a decrease in the actual number of individuals entering the population, given a stable mortality level in the juvenile stages. On the other hand it might also suggest a higher growth rate taking the toads clear of small sizes classes. At Osbaston Hall, a clear variation has been shown in total emergence of metamorphs during 1991-1994. This decline in the metamorph output appears more likely to explain the loss of the smaller and 'younger' elements of the population than any increase in sub-adult mortality or change in the rate of growth.

6.4.4 Sex ratio

The breeding population was biased towards males in each year, ranging from 4.4:1 in 1993 to 2.9:1 in 1994. This confirms previous studies (for example Gittins 1983c). The sex ratio was highest for the catches from the traps closest to the breeding site and

lowest at the distal sites. Adult toads orient themselves towards the pond in autumn (Sinsch 1988, Oldham and Swan 1991), an over-wintering location close to the breeding site is advantageous for the male since it may offer the opportunity to arrive at the breeding site early. The sex ratio was lowest for the catches at the greatest distance away from the breeding site. The lower sex ratio at locations further away from the site may also suggest that females disperse more widely from the breeding site prior to over-wintering than males.

The sex ratio observed in the water during breeding was higher than that estimated from the terrestrial pitfall traps. The sex ratio in the water did, however, decline during the breeding season and this pattern was observed in each year, Figure 6.14. This is expected given that males arrive at the breeding site earlier than the females, although the males' longer residency may distort this. Woodward (1984) divided the overall sex ratio by the average number of nights spent in the pond by *Bufo woodhousei* to provide the mating probability. He showed that the females were less numerous than males but showed nightly mating probabilities of 0.71-0.95 compared to a value of 0.14 for males. The lower breeding probability on each night for the males may be one of the factors that explain their longer residence at the pond during the breeding season, although males, unlike females, may breed more than once during an individual breeding season.

At Osbaston, larger males arrived at the Lake and Spur before smaller males. A similar decline in the length of toads arriving at a breeding pond during the breeding season was shown by Gittins (1983a). Early arrival by a male at the breeding pond early will increase the opportunity to secure a mate by increasing the number of available 'breeding nights' (*sensu* Woodward 1984). Males have the opportunity to pair on several occasions during the breeding season and thus, by arriving early, so the opportunity for several matings is increased. Females become unresponsive to males after spawning and will leave the pond soon after, at a suitable opportunity (Fraser 1985). The sex ratio at the breeding site is however, higher at the start of the breeding season and therefore the competition for females is higher. Later in the season there is a lower breeding sex ratio and so the nightly opportunity for a successful pairing for the male may increase. The number of remaining breeding nights is however, reduced and therefore the overall opportunity for a successful mating is decreased.

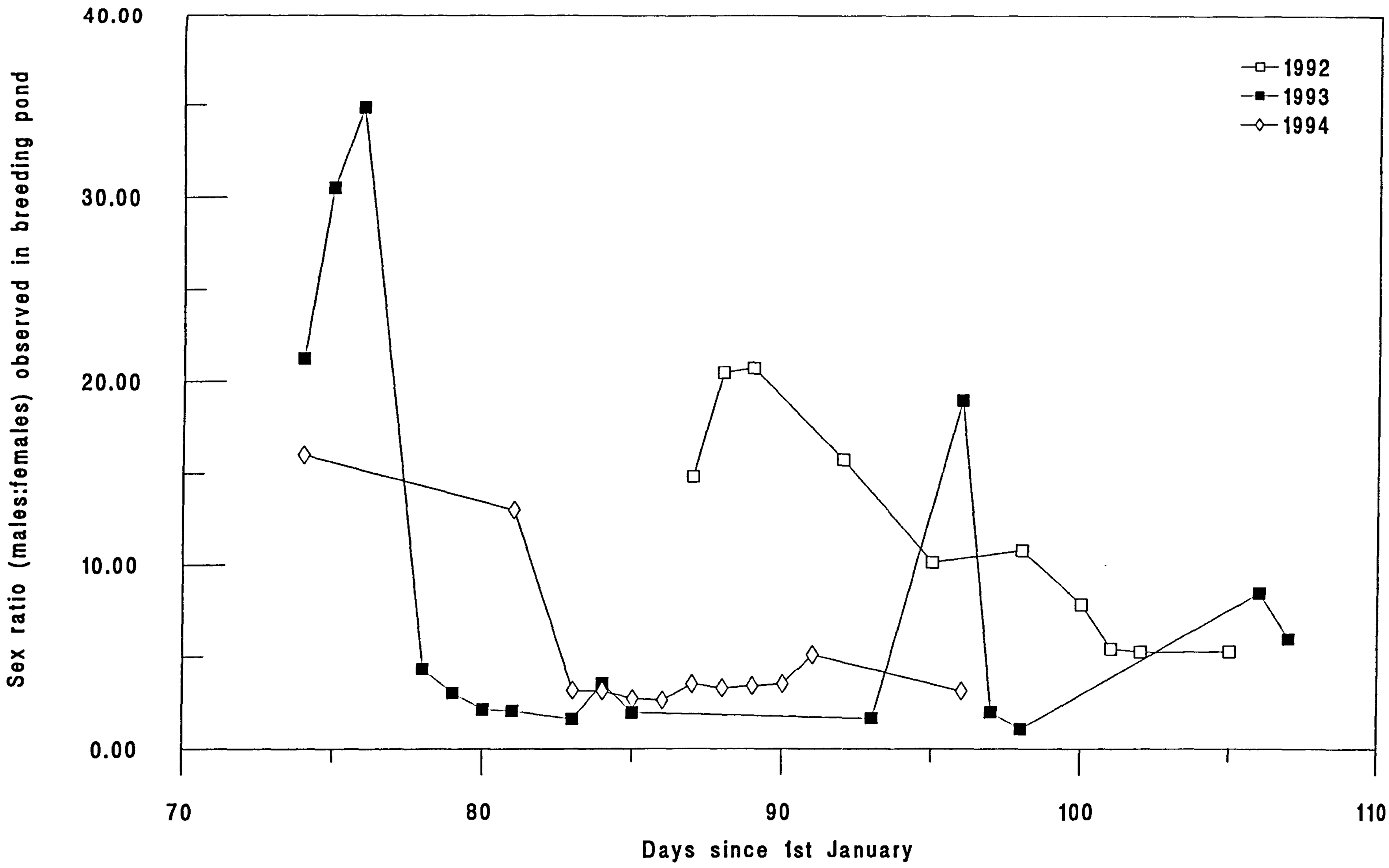


Figure 6.14: Operational sex ratio in the Lake during the breeding seasons 1992-94, Osbaston Hall.

At Osbaston, during the early part of the breeding season, the pond is dominated by large animals facing a high sex ratio. At this stage of the breeding season the smaller males would be unlikely to be successful in any encounter with a larger male for a female (*sensu* Davis and Halliday 1977). The smaller toads however, arrive at the pond later in the season, after the main influx of females, and therefore face a lower sex ratio. Under these conditions the smaller toads may have a better opportunity for a successful pairing, although the overall opportunity for breeding, in terms of the number of breeding nights remaining is reduced.

For females there is a reproductive advantage of both a larger body size and obtaining a high fecundity, hence the assumption of a uniformity in female condition from contrasting habitats. For males, although a larger size may increase the likelihood of maintaining a successful pairing, with smaller males being considered inferior (Davis and Halliday 1977), any mating that results in the fertilization of eggs can be considered to be a reproductive success. Larger males have an advantage in likely fertilisation success over smaller males due to the proximity of paired urostyles during amplexus. However, given the knots of toads that are observed at the height of the breeding season, fertilization of eggs by more than one male is clearly possible. The evidence supplied in the previous paragraph indicated a decline in the length of males during the breeding season. As the sex ratio falls and competition for females also falls, small opportunistic males may be able to fertilize eggs even if they are not the dominant male within the pairing. Inferior males adopting similar satellite strategies may be observed in cases of vocalisation, where silent animals position themselves close to larger callers and intercept females en route (Arak 1988). Beebee (1996) reports that for natterjack toads (*Bufo calamita*) larger males dominated pairings when the sex ratio was high and in favour of males. When the sex-ratio was lower virtually all males successfully paired.

There is clearly further opportunity to develop a better understanding of competition and breeding behaviour in controlled field experiments.

6.4.5 Factors affecting the breeding migration

The median date (day 80) for the breeding migration at Osbaston Hall over 1990-1994 was 16 days earlier than the timings reported in Slater *et al.* (1985) at a site in mid-

Wales (day 96) over 1978-82. The geographic locations of the two sites are likely to explain the majority of this variation, with the Leicestershire site witnessing warmer temperatures earlier in the year than the Welsh site; toads are recorded arriving at breeding sites in Dorest as early as late January and February (Reading pers. comm.). The timing of the female migration was between 2-16 days later than that for the male migration. There was no pattern observed in the date of peak water counts over the current study to indicate a change in breeding behaviour that would confirm a move to earlier breeding for the toad as observed by Beebee (1995) for two species in Sussex, Figure 6.15. Slater *et al.* (1985) reports a difference of only two days between the median dates of male and female. The difference in the timing of migration may be a result of the location of the female's over-wintering habitat and/or a later rise from over-wintering. The difference may also be influenced by the intervening temperatures, with a fall in air temperature after the male migration inflating the gap. During 1992, for example the evening temperature was below 4°C on 9 of the 16 days between the male and female median migration.

Slater *et al.* (1985) relates the consistent duration of the active toad migration to the consistent size of the breeding population; smaller populations may have a shorter breeding season purely because of the smaller mass of toads to migrate. The apparent reduction in the size of the breeding population at Osbaston Hall, especially between 1993-1994 did not however, appear to shorten the breeding season in 1994.

6.4.6 Variation in output and spatial distribution of metamorph emergence

In each year (1991-1993) metamorph emergence was characterised by a synchrony in emergence, reflected by almost 40% the total metamorphs caught during the peak of the exodus. This synchrony in emergence may be beneficial in predator avoidance, with a mass emergence producing a glut of prey too great for a predator to exploit (Beiswenger 1975).

Some caution should be placed on the results from the metamorph emergence due to sampling method. In 1991 and 1992 metamorph catches occurred on the first day of sampling. This might indicate that the initial phase of emergence could have been missed and therefore the time of emergence would be out of line, and the total

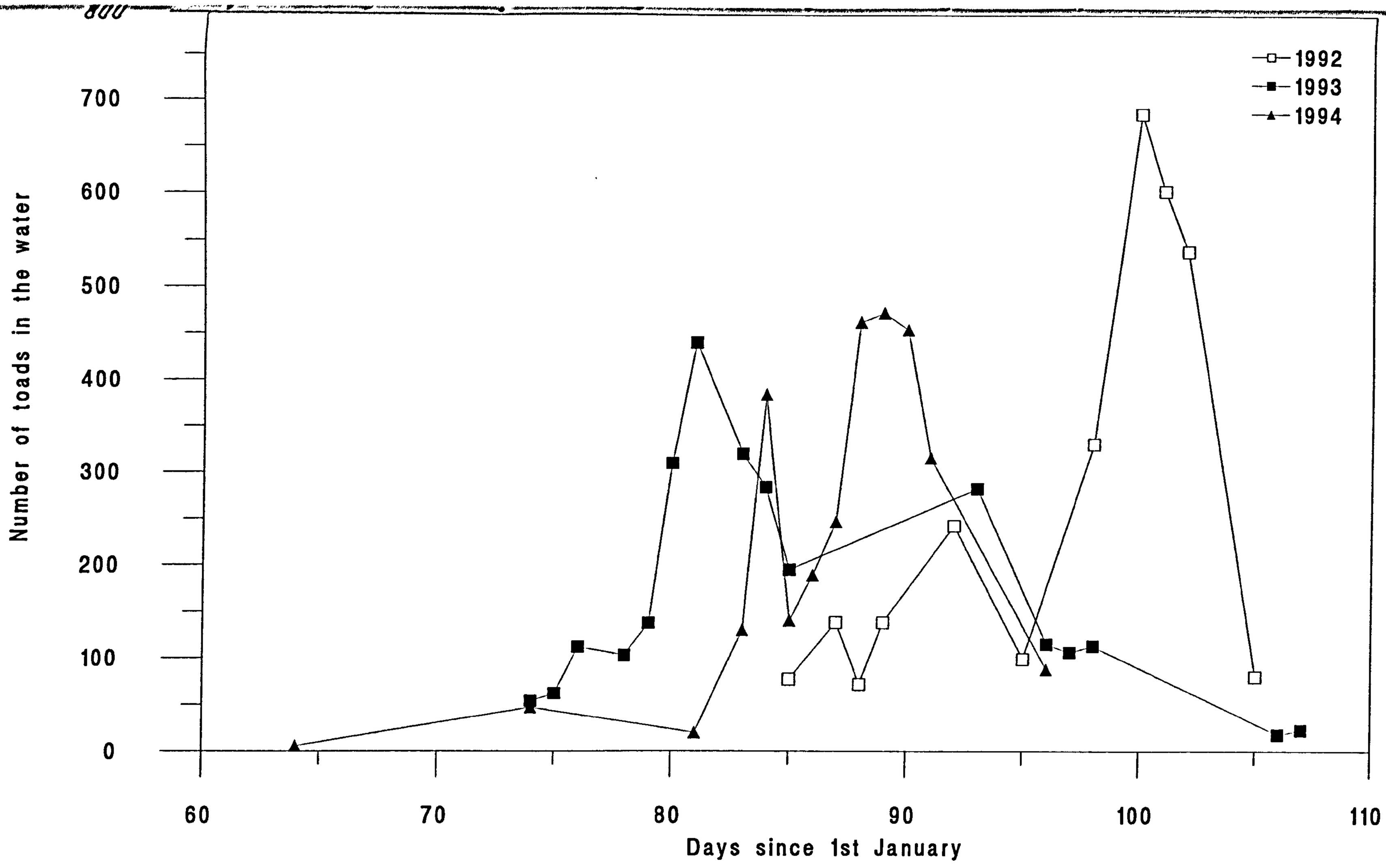


Figure 6.15: Variation in the temporal pattern of the breeding season over the study, as defined by the number of adult toads seen on during a particular night count, Osbaston Hall (Lake only) 1992-1994.

emergence for these years might, therefore, be an underestimate. In 1993 and 1994 larval development was monitored and used to indicate the commencement of trapping. In 1993, no metamorph catches were recorded until the third day of sampling, suggesting that the start of the emergence was correctly identified. In 1994, there appeared to a failure in breeding with an estimate of less than 2000 metamorphs emerging from the breeding site (both the Lake and the Spur).

There is evidence that metamorphs remain close to the edge of the pond during the first days after emergence (Oldham pers. comm.). If this is the case, then animals that evaded capture during their actual emergence may have been caught during the time they remain close to the pond edge. Although the impact of this cannot be quantified, given the nature of the traps used at Osbaston Hall, it suggests that total emergence is inflated. In addition, there has been evaluation of the impact of the weather conditions during the emergence, and these are likely to influence the behaviour of the metamorphs. During dry conditions metamorphs may stay close to the pond edge to prevent desiccation, rain may encourage dispersion. These factors may have an impact on the catches in the traps, particularly the catches of previously emerged metamorphs during drier conditions.

6.4.7 Changes in the magnitude and spatial pattern of emergence

Metamorph output in 1991 and 1994 was particularly low, despite high breeding counts. The highest output of 220,000 ± 10,000 metamorphs in 1993 may be compared to 100,000 at a site in mid-Wales (Slater 1992) and 500,000 for a site in north-west Leicestershire (extrapolated from Oldham 1985). The breeding population at Osbaston Hall was estimated at 4000 compared to 8600 adults for the site in mid-Wales (Gittins 1983) and 7000 for Oldham's site in Leicestershire (Oldham 1985). The metamorph output per adult at Osbaston (55 metamorphs/adult) was higher than in Slater's study (12 metamorphs/adult) but lower than Oldham's site (71 metamorphs/adult). No data were available on the variability of metamorph catches for comparison.

Smithson (1991) reported that 50% of the sampled emergence from Osbaston lake in 1990 occurred on LE, with just less than 40% occurring on LW. Only 10% emerged from LN and LS combined. In comparison to these data, the proportion of the total

emergence from LN and LE declined through the study, whilst the proportion from LS remained consistently low and the proportion from LW increased (except in 1994). The decline of the breeding night count and spawning activity on LE may partly explain the observed decline in the number of metamorphs, although it is unclear why the bank has declined in suitability. The loss of the intensive trapping on the eastern site of the lake makes it difficult in establish if there was a decrease in the number of toads entering the lake from this direction, which might reduce the number of individuals spawning at this location. However, toads are known to move through a waterbody in search of a suitable spawning location (Oldham pers. comm.). Decline in water quality has also been shown to reduce the productivity (in terms of metamorph output) of breeding sites (Oldham and Swan 1991) and if animals showed a tenacity to their point of emergence for breeding the observed decline would be consistent.

The output of the Spur has been consistently low, the highest output of only 4000 ± 170 animals in 1992. Despite spawning and evidence of tadpoles throughout May, tadpoles in the Spur declined in abundance rapidly during June of each year. The reasons for this are unclear, although casual observation by Watt (pers. comm.) suggest that tadpoles may move to the centre of the water body and appear less visible, and may be missed in the bottle traps placed on the perimeter of the Spur. Catch results, however, in the metamoprh traps still indicate that fewer animals successfully reached metamorphosis in the Spur than the Lake. Common frogs spawn in both the Lake and the Spur, selecting the south-east corner of the Spur as a preferred spawning location (Latham, unpublished). During the course of the current study there was a consistent output of frog metamorphs from the Spur during 1991-1994 (Latham, unpublished). The Spur is shaded by alders and the pond has a deep layer of sediment. Increased biological action during high summer temperatures could induce a sudden fall in the oxygen levels of the water during the development of the tadpole and there is some evidence to support a fall in dissolved oxygen in the Spur (Norris 1994). Toad tadpoles do not develop lungs until late in their larval development (Slater 1992); in contrast to frog tadpoles that develop lungs earlier and also emerge earlier. Whilst a sudden fall in dissolved oxygen would lead to mortality for the toad, since they absorb oxygen through gills, frog tadpoles could, however, survive by changing respiratory behaviour and breathing on the surface.

The poor output from the Spur over the course of the current study might partially explain the decline in the number of toads caught in the Rookery. Metamorphs emerging from the natal pond are believed to disperse into the surrounding landscape in a random fashion, moving out at right angles to the pond (Oldham 1985). The Rookery is to the south of the breeding ponds, closest to the Spur. Poor output from the Spur over successive years would reduce juvenile input into the Rookery. This assumes, however, that the Spur did successfully produce metamorphs in previous years and that is unknown. In addition, there are no known reasons that could explain why the Spur should become unfavourable for tadpoles over the last four years.

Chapter Seven: Terrestrial habitat use by the common toad

7.1 Introduction

The evaluation of the use of available habitats by the toad was undertaken by studying habitat use at the population level, through a combination of drift fences and pitfall traps and by individuals, using radio-tracking techniques. This chapter presents the results from the studies undertaken at Osbaston Hall (1991-1994) supplemented by studies at the radio-tracking enclosure at Coleorton (1992) and Little Wittenham Nature Reserve (1994-995). The objectives of the studies were four-fold. First, to quantify the density of toads found in a variety of agricultural habitats. Second, to establish the time budgets exhibited by the toad for each habitat. Third, to evaluate the effect of normal agricultural practice on habitat use by the toad, and finally to establish the factors that influenced activity, density and habitat use.

The extensive trapping studies conducted during the spring migration were used to estimate the over-wintering and summer densities of toads. Habitats were defined by their general habitat general characteristics (woodland, pasture, hedge, arable etc.), where preference was indicated by adult density (Chapter 6). Radio-tracking studies, conducted during the summer terrestrial phase of the adults, were undertaken to provide data on individual habitat use. Habitat use was addressed by determining the length of time spent in each of the habitats and the number of radio-fixes located in each of the habitats.

7.2 Results

7.2.1 Vegetation form and available cover

The habitats at the Osbaston Estate and the enclosure at Coleorton were classified using the National Vegetation Classification (NVC), although this proved to be unsuitable as the habitats were largely artificial in both the enclosure and arable areas at Osbaston Hall. The physical structure of each habitat classified in terms of the percentage cover at 5 levels 0-10 cm, 10-100 cm, 1-5 m, 5-10 m and above 10m. For the current study, the NVC classification of the habitat was considered to be less useful than the physical structure of the habitat for the objectives of the current study.

The woodlands at Osbaston (Rookery, Poplar Plantation, Wood) were characterised by percentage cover within each of the vegetation levels, whilst the arable and intensively managed habitats provided dense cover only within the lowest layer, Table 7.1. However, there was distinct variation in the lower layers of the woodland habitat at Osbaston. The Rookery was dominated by a ruderal and tall herb understorey, providing limited ground cover, that was atypical of a woodland and indicative of its past use as a formal garden, Figure 7.1. The Poplar Plantation showed a denser and more diverse ground cover, Figure 7.2. The woodland scrub within the enclosure at Coleorton lacked the upper canopy layers found in the woodland habitats at Osbaston Hall, although its form was noticeably different from the remaining habitats within the enclosure, Table 7.1b.

7.2.2 Adult density

7.2.2.1 Density in contrasting habitats

Chapter Six discussed the spatial distribution of catches at Osbaston Hall during the breeding. Adult density in those habitats with a HSE (Habitat Specific Enclosure) was calculated based on nett catch and area of the enclosure (PPI, RKI WDI, HDI). The density estimates for the HSEs are assumed to represent the summer densities, since the fences were constructed and made 'toad-proof' during the late summer prior to any migration that might occur prior to over-wintering. The density in those habitats served by a drift fence (AN, AW) was calculated based on the length of the drift fence and the number of captures per metre.

Toad density was higher in the woodland habitats than the neighbouring pasture and arable habitats throughout the study, Table 7.2. The highest densities were estimated for the Poplar Plantation and the Hedge within the Rough East Complex, in each year of the study. The estimated density in the arable areas was consistently the lowest for all of the study habitats. In 1994, the adult density[1] observed in the deciduous blocks at Little Wittenham (430 toads/ha ± 110) was comparable to that observed at

[1] Densities are provided with confidence interval based on density estimates from each of the enclosures.

TABLE 7.1: Vegetation structure gained from point-quadrat locations within each habitat at Osbaston Hall. Surveys were completed during June-July 1991.

Habitat	Mean percentage cover/quadrat				
	0-0.1m	0.1-1m	1-5m	5-10m	10m +
Wood copse	67.0	60.6	58.6	42.6	49.8
Rookery	25.2	95.5	32.5	28.0	18.6
Poplars	95.5	95.5	8.2	10.6	55.8
Rough pasture	95.5	90.5	0.0	0.0	0.0
Arable -wheat	60.0	79.0	0.0	0.0	0.0
Arable - root	4.6	1.6	0.0	0.0	0.0

TABLE 7.1b: Vegetation structure gained from point-quadrat locations within each habitat of the test-enclosure at Coleorton. Surveys were completed during June-July 1991. Vegetation did not extend to above 5m.

Habitat	Mean percentage cover/quadrat			
	0-0.1m	0.1-1m	1-5m	5-10m
Wood scrub	42.0	62.7	18.2	0.0
Rough pasture	95.5	95.5	0.0	0.0
Improved pasture	84.0	90.5	0.0	0.0
Cultivated	22.0	18.7	0.0	0.0

Figure 7.1: Rookery ground vegetation, dominated by ruderal herbs with bramble and horsetail in the damper areas. May 1994.

Figure 7.2: Poplar plantation ground vegetation, dominated by nettle and hogweed. May 1994.

TABLE 7.2: Estimated density (toads/hectare) for Osbaston Hall, 1991-1992. Where the data are associated with a drift fence the density has been calculated by extrapolation of the trapline density and the are of the habitat. Densities have not been corrected for fence efficiencies.

	Location	1992		1993		1994	
		Catch/m	Density	Catch/m	Density	Catch/m	Density
Poplars	25m	1.78	1260	2.22	1530	1.73	1220
Rookery	250m	0.90	630	0.60	420	0.29	205
Wood	175m	0.32	200	In operative		In operative	
Hedge	200m	0.33	1830	0.38	2200	0.23	1400
Spinney	400m	0.58	140	0.44	120	0.28	40
Pasture	160m	1.49	200	In operative		In operative	
Arable (W)	100m	1.79	58	1.19	40	1.39	50
Arable (N)	210m	0.42	50	0.20	20	0.14	16

TABLE 7.2b: Adult density (raw and adjusted) for coniferous (C1-C3) and deciduous habitats (D1-D4) at Little Wittenham Nature Reserve 1994. 1: Estimated through the geometric relationship between the size of the enclosure and sample area (see Chapter 6). 2: Adult toads per hectare. 3: Adjusted density extrapolated from the catch and multiplied by the correction factor.

Habitat	Distance from pond	Correction factor[1]	Density[2]	
			Raw	Adjusted[3]
Scrub	75	1	380	380
Conifer plantation	150	2	31	64
Conifer plantation	225	3	63	191
Mature coppice	75	1	540	540
Mature coppice	150	2	414	828
Mature coppice	225	3	34	190
Mature coppice	300	4	254	1019

Adult density (raw and adjusted) for coniferous (C1-C3) and deciduous habitats (D1-D4) at Little Wittenham Nature Reserve 1995. 1: Estimated through the geometric relationship between the size of the enclosure and sample area (see Chapter 6). 2: Adult toads per hectare. 3: Adjusted density extrapolated from the catch and multiplied by the correction factor.

Habitat	Distance from pond	Correction factor[1]	Density[2]	
			Raw	Adjusted[3]
Scrub	Not functional in 1995			
Coppice plantation	150	2	64	127
Coppice plantation	225	3	96	287
Mature coppice	75	1	382	382
Mature coppice	150	2	191	382
Mature coppice	225	3	32	96
Mature coppice	300	4	191	764

Osbaston Hall (200-500). The deciduous woodland at Little Wittenham supported a higher toad density than the coniferous blocks (150 ± 54), Table 7.2b. In 1995, the catch fell slightly at Little Wittenham, resulting in a lower estimated density for both the deciduous (199 ± 122) and coniferous (80 ± 23) habitats, despite this the ratio between the number caught in the deciduous and coniferous habitats was similar. As discussed in Chapter 6, the fence efficiency at Little Wittenham was estimated to be 90% and therefore the density estimates at this site are likely to be more reliable than those at Osbaston Hall, where the fence efficiency was only 50-60%.

A significant positive correlation ($n = 98$, $r = 0.378$, $p < 0.01$) was obtained comparing the adult density with survival adult, whilst a negative correlation was obtained comparing the distance of the habitat from the breeding site ($n = 98$, $r = -0.588$, $p < 0.01$), Table 7.3. Density was also positively correlated with the percentage cover, particularly at Level 1 (0-0.1m), Level 2 (0.1-1m) and Level 5 (10m+), Table 7.3. There were no significant correlations observed between adult density and the remaining variables; adult condition, length, mass and mean age.

7.2.3 Habitat fidelity

Fidelity to terrestrial habitat at Osbaston is shown in Tables 7.4a - 7.4c, for the periods 1991-92, 1992-93, 1993-94. Fidelity to habitat was highest in the Rookery, the sole enclosure to the south of the breeding ponds in 1991-92 and 1992-3. In 1993-94, the Rookery percentage was slightly lower than the previous years (83%), with an increase in the number of Rookery animals found in the Poplar catch. Fidelity was also high at the Spinney trapline, the most distant fence from the breeding ponds, although no recaptures marked from the Spinney were caught in 1994. The Wood enclosure was only operational during 1991-92 and only one value could be calculated.

Fidelity in the Poplar Plantation HSE was consistently lower than 60% throughout the study. The relatively low fidelity for this enclosure could, in part, be attributed to the location of the Poplar enclosure which was close to the breeding site. The Poplars was on the line of toad migration to the ponds, and therefore untagged toads

TABLE 7.3: Correlations between adult density in available habitats over 1992-94 with various variables, Osbaston Hall 1: Product moment correlation. 2: N = 98.

Variable	r value [1]	p value [2]
Mass	-0.195	NS
DLU	-0.226	NS
Condition	-0.047	NS
Age	-0.203	NS
Level 1	0.741	p <0.01
Level 2	0.445	p <0.01
Level 3	0.239	NS
Level 4	0.312	p <0.05
Level 5	0.900	p <0.01
Survival	0.378	p <0.01
Distance	-0.588	p <0.01

TABLE 7.4a: Comparative fidelity to the 5 habitats, Osbaston Hall 1992. Figures represent the percentage of toads recaptured in 1992 years on their approach to the breeding site. The bold text represents the fidelity exhibited by the toads to their former over-wintering habitat, ie marked then recaptured in the same habitat over successive years.

	Location of recapture in 1992				
Mark in 1991	**Poplar**	**Rookery**	**East**	**Spinney**	**Wood**
Poplar[1]	**55**	5	1	34	6
Rookery[2]	1	**93**	1	0	5
East[3]	8	5	**83**	0	3
Spinney	0	9	0	**91**	0
Wood	8	0	22	23	**46**

TABLE 7.4b: Comparative fidelity to the 5 habitats, Osbaston Hall 1993.

	Location of re-capture in 1993			
Mark in 1992	**Poplar**	**Rookery**	**East**	**Spinney**
Poplar	**60**	11	28	1
Rookery	4	**96**	0	0
East	3	1	**90**	6
Spinney	3	1	6	**91**

1: Poplar catch represents the combined catch from inside and outside the polar enclosures and the arable west drift fence. 2: Both inside and outside the rookery enclosure. 3: East catch represents all the eastern hedges and arable north.

TABLE 7.4c: Comparative fidelity to the 5 habitat enclosures, Osbaston Hall 1994. Figures represent the percentage of toads recaptured in 1994 years on their approach to the breeding site. The bold text represents the fidelity exhibited by the toads to their former over-wintering habitat, ie marked then recaptured in the same habitat over successive years.

	Location of re-capture in 1994			
Mark in 1993	**Poplar**	**Rookery**	**East**	**Spinney**
Poplar	**54**	14	0	32
Rookery	13	**83**	3	1
East	0	4	**96**	0
Spinney	0	0	0	**0**

1: Poplar catch represents the combined catch from inside and outside the polar enclosures and the arable west drift fence. 2: Both inside and outside the rookery enclosure. 3: East catch represents all the eastern hedges and arable north.

TABLE 7.5: Division of 1994 poplar recaptures into location of first tag, ie 13% of recaptures in the poplar habitat showed tags indicating a first catch in the poplars in 1991.

Habitat	**First tag location**		
	1991	**1992**	**1993**
Poplars	13	23	35
Rookery	<1	1	1
East	<1	4	5
Spinney	4	<1	0
Wood	6	1	0

trespassing into the Poplar enclosure[2], and being caught within the HSE, would incorrectly be tagged as Poplar toads. This might help to explain the decline in the percentage of recaptures for the Rookery in 1993-994, and the increase in the trespass of the Poplar HSE, Table 7.4c. Review of all the recaptures for the Poplars (PPI) over each year of the current study did show, however, that the animals tagged for the first time in the Poplars consistently formed the highest proportion of the identified recaptures, Table 7.5.

The fidelity shown by the adults to previous home ranges at Osbaston is consistent with the limited results available at Little Wittenham where four of the 200 toads marked in 1994 were recaptured in 1995 in the habitats where they had been marked during the previous year. Those animals caught in the deciduous woodland (n = 3) were recaptured in the same enclosure as the previous season. Given that the total area of an enclosure was less than 300m^2, this is of particular interest.

7.2.4 Habitat use by the individual - Radio-tracking studies and night searches

7.2.4.1 Fate of the tracked toads

In 1992, 24 (15 females and 9 males) were released into the enclosure, Coleorton, Table 7.6. One toad (number 003) was predated by a Magpie (*Pica pica*) after less than 24 hours in the enclosure. The remaining animals were released and followed for periods between 25-50 days then recaptured and returned to tanks until they regurgitated their tag. Four animals (numbers 009, 012, 017 and 022) were lost despite retrieving the radio-tag, one animal (018) had also regurgitated its tag but was found within centimetres of it. In four cases (011, 013, 014 and 015) both the toad and the tag were lost, despite thorough searches.

In 1994, 24 toads were released at Osbaston Hall, twelve in the Rookery and twelve in arable fields, Table 7.7. The animals were tracked for periods between 12-27 days then recaptured and returned to tanks until they regurgitated their radio-tags. Four toads (501, 503, 505 and 516) were predated; chewed toad carcass were found close

[2] It was known that the fences were not 100% efficient.

Table 7.6: Summary of toad details for the tracking period Day 181 to 294, 1992. DLU: Dorsal length to urostyle. % Change in mass over release period. Days since 1/01/92. NK: Not known

Toad	Sex	DLU (mm)	Release mass (g)	Re-capture mass (g)	% Change	Rention time (Days)	Release period (days)	Notes
92001	Female	56.0	22.3	25.8	15.7	25	181 - 205	Toad collected
92002	Female	65.5	25.1	42.1	67.7	25	181 - 205	Toad collected
92003	Female	62.0	27.6	NK	NK	NK	181 - 182	Predation
92005	Female	62.5	25.1	31.7	27.1	32	181 - 205	Toad collected
92007	Male	59.0	19.1	26.3	31.7	34	181 - 205	Toad collected
92008	Female	69.0	32.2	48.3	50.0	35	196 - 233	Toad collected
92009	Male	62.5	25.9	NK	NK	18	196 - 215	Toad lost
92010	Female	63.0	28.2	NK	NK	24	215 - 238	Toad collected
92011	Female	62.0	29.2	36.6	21.4	>16	222 - 238	Toad & tag lost
92012	Male	55.0	23.3	NK	NK	15	222 - 237	Toad lost
92013	Female	68.5	40.7	49.4	21.4	>16	222 - 238	Toad & tag lost
92014	Female	58.0	21.2	25.1	18.4	>16	222 - 238	Toad & tag lost
92015	Female	59.5	23.0	25.3	10.0	>15	223 - 238	Toad & tag lost
92016	Female	67.0	37.2	45.2	21.5	34	225 - 254	Forced rejection
92017	Male	64.5	30.1	35.5	9.9	13	225 - 238	Toad lost
92018	Male	60.5	29.3	35.3	31.7	34	225 - 254	Field rejection
92019	Female	69.5	35.4	31.6	-10.7	26	254 - 272	Toad collected
92020	Female	61.5	24.4	27.2	-5.3	28	254 - 272	Toad collected
92021	Male	62.0	26.1	34.2	31.0	27	254 - 281	Toad collected
92022	Male	60.0	23.8	NK	NK	27	254 - 269	Toad lost
92023	Male	60.5	24.9	23.1	11.6	15	254 - 272	Toad collected
92024	Male	57.5	64.5	21.3	-11.6	27	254 - 272	Toad collected
92025	Female	65.5	34.6	34.6	0.0	52	273 - 294	Toad collected
92026	Female	64.5	36.0	35.7	-0.8	58	273 - 294	Toad collected

Table 7.7: Summary of female toad details for the tracking period 159-240, Osbaston 1994. DLU: Dorsal length to urostyle. 1 = release mass (g). 2 = recapture mass (g). 3 = tracking period (days since 1/01/94). NK: Not known

Toad	Habitat	DLU (mm)	Release mass (g)	Re-capture mass (g)	% Change	Rention time (Days)	Release period (days)	Notes
94501	Arable West	695	52.7	54.7	3.8	NK	159 - 186	Predated
94502	Arable West	705	55.4	NK	NK	NK	159 - 165	Toad and tag lost
94503	Arable West	695	55.1	59.2	7.4	< 20	165 - 185	Predated
94504	Arable West	650	31.8	42.5	33.7	20	165 - 185	Toad tost
94505	Arable West	670	38.9	39.7	2.1	< 15	165 - 180	Predated
94506	Rookery	670	41.9	NK	NK	11	187 - 208	Toad lost
94507	Rookery	665	44.9	38.8	-13.6	23	187 - 208	Toad collected
94508	Rookery	630	35.6	34.5	-3.1	25	187 - 208	Toad collected
94509	Rookery	630	38.8	NK	NK	21	187 - 208	Toad lost
94510	Rookery	610	35.2	37.2	5.7	35	165 - 180	Toad collected
94511	Rookery	640	30.0	28.5	-5.0	24	165 - 180	Toad collected
94512	Rookery	680	42.1	44.9	6.7	23	165 - 180	Toad collected
94513	Rookery	610	37.5	34.2	-8.8	22	165 - 180	Toad collected
94514	Arable West	625	46.6	35.2	-24.5	20	195 - 208	Toad collected
94515	Arable West	670	36.6	NK	NK	< 13	195 - 208	Toad and tag lost
94516	Arable West	680	40.4	NK	NK	< 15	196 - 211	Predated
94517	Arable West	670	38.2	35.0	-8.4	27	196 - 208	Toad collected
94518	Arable West	640	30.3	NK	NK	36	224 - 240	Toad collected
94519	Arable West	680	34.9	NK	NK	< 16	224 - 240	Toad and tag lost
94520	Rookery	640	26.4	30.9	5.1	22	224 - 240	Toad collected
94521	Rookery	680	33.9	37.2	9.7	18	224 - 240	Toad collected
94522	Rookery	655	28.5	30.2	5.9	14	228 - 240	Toad collected
94523	Rookery	640	27.1	25.8	-4.8	19	228 - 240	Toad collected
94524	Arable West	675	35.3	NK	NK	< 16	224 - 240	Toad and tag lost

to the radio-tag and it was assumed that these toads were victims of rats or possibly weasels, numerous on the estate. Similar chewed carcasses were observed at pitfall traps and along drift fences during the breeding seasons (pers. observation). Three animals (504, 506 and 509) were lost despite retrieving the radio-tags, and in four cases (502, 515, 519 and 524) both the toad and the tag were lost. The four toads lost with their tag were released in the arable fields. Although toads were lost in the Rookery (506, 509) their tags were collected. Losses of both the toad and radio-tag are frustrating since it is impossible to attribute the loss of the toad to tag failure, predation or wandering out of range. Similar frustration was experienced in other radio-tracking studies (Brown 1991, Denton 1991, Oldham and Swan 1992).

7.2.4.2 Release behaviour

Some toads released into the enclosure at Coleorton were observed to move towards the perimeter of the enclosure and repeatedly move up and down the fence with successive radio-locations following the fence line following the first few hours after release. Others took refuge under surface debris. Three toads escaped from the enclosure (002, 005 and 009) during the first few days after release. The perimeter fence was improved after initial escapes and no further animals were confirmed to have escaped. The width of the enclosure, a distance of 30m, could be covered by a toad within 2-3 hours of release.

In the free-ranging animals at Osbaston Hall, twenty-two, of the twenty-four toads retreated to a hiding place close to the release point (with 15m) immediately after release and remained unmoved for periods of 2 to 14 days. One toad (511) was lost in the arable field after the first night of tracking, between 4.00am and 10.00am assumed lost, but relocated 200m from the release point four days later where it remained for two nights before being lost permanently. Of the twenty-two toads that retreated to a hiding place immediately after release, two toads (515, 520), remained unmoved for over a week, but then lost. In both cases the toads had remained unmoved for at least 12 hours during one evening's tracking, but could not be located the following morning. These radio-tags were reaching the end of their effective lives, and it is known that signal strength does not decline consistently over age (Cresswell pers. comm.). However, despite searches the toads could not be found and it appears

that this animals were probably lost due to tag failure.

7.2.4.3 Home ranges

For the radio-tracked animals, the home range was calculated using the minimum convex polygon (MCP) method, where the area of the home range is determined by joining the outer fixes. At Little Wittenham Nature Reserve, home range was determined using Loman (1994).

For the toads released into the enclosure, the toad lost to predation (003) and two toads (025, 026) released late in the season (October 92) were removed from analysis. Toad number (003) was lost in predation after only one day in the enclosure, and the toads released late in the season buried themselves throughout the tracking period. For the females released at Osbaston Hall, home range estimates were calculated for the Rookery, the arable areas. The home ranges were the largest in the females released into the Rookery at Osbaston (5602 ± 1472m^2, n = 12, range 1840m^2 - 6323m^2) and smallest for the females released into the enclosure at Coleorton (400 ± 81m^2, n = 12, range = 256m^2 - 1135m^2), see Table 7.8. The home range for males released into the enclosure was calculated as 540 ± 110m^2 (n = 9, range 275m^2 - 932m^2). The home range estimated for females released into the enclosure was smaller than that observed for males, although the difference was not significant. The home range estimated for females released into the arable habitat (4161 ± 3064m^2, n = 12, range 320m^2 - 5734m^2) was smaller than for the Rookery, but showed a high standard deviation.

The home ranges calculated for the enclosure at Coleorton should be treated with some caution since animals were not permitted to wander freely, and restricted within the enclosure itself. Despite the mean home range for toads released into the enclosure being significantly less that the total area of the enclosure (850m^2), it is uncertain what impact, if any, this restriction had on toad movement.

At Little Wittenham the home range estimate (Loman 1994) for toads utilising the coniferous woodland (admittedly based on only 1 individual) was larger that those that used the deciduous woodland (n = 3).

TABLE 7.8: Home range calculations for adult toads released into the enlcosure (males and females), Coleorton 1992 and into the arable fields and Rookery (females only), Osbaston 1994.

Habitat/location	Age	Sex	N	Home range (m^2)
Test-enclosure[1]	Adult	M	9	540 ± 110
Test-enclosure[1]	Adult	F	12	400 ± 81
Arable[1]	Adult	F	12	4161 ± 3064
Rookery[1]	Adult	F	12	5602 ± 1472
Coniferous woodland[2]	Adult	M	1	1500
Deciduous woodland[2]	Adult	M	3	300

1: MCP using radio-fixes. 2: Based on minimum area circle area encompassing recapture points (Loman 1995)

7.2.4.4 Analysis of habitat usage within the enclosure

In total, 1139 radio-fixes were recorded for the 21 toads released into the enclosure, Coleorton. Comparison of the area of each of the habitats within the enclosure and the percentage of the total number of radio-fixes located in each of the habitats illustrated the predominance of radio-locations (fixes) in the wood scrub for both males and females, Table 7.9. For males, nearly 50% of the radio-fixes were located in the wood scrub. This figure does not adjust the percentages for habitat availability.

To adjust for availability and indicate preference a comparison was made of the proportion of each habitat and the total area of the enclosure with the proportion of fixes within each habitat and total number of fixes (Neu *at el.* 1974). Table 7.10 shows analysis for toad number (021). Initially a chi-squared test was calculated, as a test for homogeneity. The level of observed use of each habitat was compared with its availability through a Bonferroni ***z*** statistic, and confidence intervals were built around the observed use of each available habitat (Neu *at el.* 1974). If the chi-squared value calculated for the habitat is below the lower confidence limit, the habitat was used at the level lower than its availability (avoidance), and if the value is above the higher confidence limit the habitat was used over and above its availability (preference). Toads illustrated a significant chi-squared result indicating that the fixes were not randomly dispersed through the enclosure, Table 7.11. In ten of the cases the woodland habitat was shown to be selected above confidence intervals calculated and in thirteen of the cases the cultivated habitat was shown to be selected under the identified confidence intervals, Table 7.11. Selection of the rough habitat was undetermined with ten toads showing neither preference nor avoidance. Selection of the improved grassland was variable with seven toads favouring the habitat and four toads discarding the area.

Aebischer, Robertson and Kenward (1993) question the use of preference/avoidance tests based upon chi-squared analysis, since the 'avoidance' of one habitat type will almost invariably lead to apparent preference for another. To examine the selection of the toad home ranges from within the enclosure, the relative proportions of each of the habitats in the MCP home ranges were compared with the proportions in the total study area. Habitat use within the home range was assessed by taking the

TABLE 7.9: Percentage area of habitat types within the tracking enclosure, Coleorton (total mapped area = 100%) and the percentage of the total number of fixes in each habitat by male and female common toads.

	Proportion of enclosure	Habitat	
		Male (n=9)	Female (n = 12)
Wood scrub	19.8	49.7	43.6
Rough pasture	26.7	13.4	17.3
Improved pasture	24.9	27.9	18.4
Cultivated	24.6	7.8	18.3
Hedge	4.0	1.3	2.4

TABLE 7.10: Distribution of radio-fixes for toad 92021, indicating preference to the wood scrub habitat, Coleorton. Pi: the proportion of total area. Po: the proportion of radio-fixes observed. Expected frequency represents the number of radio-fixes occurring if utilisation is in exact proportion to habitat availability. The confidence interval represents the theoretical proportion of occurrence and is compared to the corresponding Pi to determine if the hypothesis of proportional use is accepted or rejected i.e. Po=Pi.

Habitat	Area (m^2)	PI	Observed	Expected	Po	Confidence interval
Wood	165	0.198	107	24	0.863	0.791 - 0.935
Cultivated	205	0.246	13	30	0.131	0.041 - 0.169
Improved	207	0.248	2	31	0.016	0.000 - 0.043
Rough	222	0.267	1	33	0.008	0.000 - 0.026
Hedge	34	0.041	1	5	0.008	0.000- 0.026

Table 7.11: Summary of preference tables (after Neu *et al.* 1974). NS indicates no significance.

Toad	Sex	Period tracked	Chi-squared value	Favoured habitat	Rejected habitat
92001	Female	30/06/92-24/07/92	24.92 ($p < 0.01$)	Improved grassland	Woodland/cultivated
92002	Female	30/06/92-24/07/92	27.10 ($p < 0.01$)	Woodland	Improved grassland
92005	Female	30/06/92-24/07/92	23.50 ($p < 0.01$)	Improved grassland	Woodland
92007	Male	30/06/92-24/07/92	11.34 ($p < 0.05$)	Woodland	Cultivated
92008	Female	15/07/92-04/08/92	167.11 ($p < 0.01$)	Woodland	Improved grass/rough
92009	Male	15/07/92-04/08/92	110.44 ($p < 0.01$)	Woodland	Cultivated/rough
92010	Female	03/08/92-26/08/92	50.50 ($p < 0.01$)	Cultivated	Grass/rough
92011	Female	10/08/92-26/08/92	53.50 ($p < 0.01$)	Improved grassland	Woodland/cultivated
92012	Male	10/08/92-26/08/92	34.37 ($p < 0.01$)	Improved grassland	Woodland/cultivated
92013	Female	10/08/92-26/08/92	11.70 ($p < 0.05$)	NS	Woodland/cultivated
92014	Female	10/08/92-26/08/92	13.60 ($p < 0.01$)	Rough	NS
92015	Male	11/08/92-26/08/92	29.25 ($p < 0.01$)	Woodland	Cultivated
92016	Female	13/08/92-11/09/92	44.13 ($p < 0.01$)	Improved grassland	Woodland/rough
92017	Male	13/08/92-11/09/92	46.20 ($p < 0.01$)	Woodland	Cultivated/rough
92018	Male	13/08/92-11/09/92	25.97 ($p < 0.01$)	Woodland	Cultivated
92019	Female	11/09/92-29/09/92	121.17 ($p < 0.01$)	Woodland	Cultivated/improved grass
92021	Male	11/09/92-29/09/92	340.77 ($p < 0.01$)	Woodland	Cultivated/grass/rough
92022	Male	11/09/92-29/09/92	166.83 ($p < 0.01$)	Improved grassland	Wood/cultivated/rough
92024	Male	11/09/92-29/09/92	42.70 ($p < 0.01$)	Improved grassland	Cultivated/rough
92025	Female	30/09/92-21/10/92	151.15 ($p < 0.01$)	Woodland	Improved grass/rough
92026	Female	30/09/92-21/10/92	18.59 ($p < 0.01$)	Rough	Woodland

proportions of each habitat within the MCP home range as describing the available habitat and comparing it with the distribution of radio-fixes within the home range (*sensu* Aebischer and Robertson 1992).

Following the standard method described by Aebischer and Robertson (1992), comparison of habitat use can be undertaken by calculating the logratio differences for all possible pairs of habitat types and producing a matrix. Table 7.12 shows habitat use of the five habitats within the enclosure by an adult female toad number (014). The Wood habitat is ranked the highest and used proportionally more than the remaining habitats. The improved pasture is ranked the lowest in terms of its use. A matrix was constructed for each animal (Tables shown in Appendix 8), and the mean and standard error calculated for each element of the matrix. Tables 7.13a and 7.13b represent the combined data for female and male toads released into the enclosure. For both sexes the rough pasture and the wood scrub proved to be the habitats most-used. None of the preferences were statistically significant[3] for the female, (indicated by a tripling of the sign in Tables 7.13a and 7.13b) implying that the differences between the habitat rankings were not greater than could be expected purely by chance. However for males the cultivated and improved habitat were significantly under used relative to the hedge and the rough. Ranking of the enclosure habitats on the basis the proportion of each habitat within the toads' home range, suggests that for the males, woodland and rough pasture were favoured over the improved grassland, cultivated area and hedge.

When comparing the number of fixes within each habitat and the proportion of the habitat within each MCP, there was again, no significant difference between the ranked habitats for the females, Table 7.13b. For the males, the woodland habitat was ranked 1, with a significantly higher use than the cultivated and rough habitats. The proportion of the hedge habitat included within the home range was used to a lesser extent (as defined by the number of radio-fixes) than the cultivated and improved habitats, implying that although the hedge was included with the home

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[3] Significance is indicated as a departure of the mean ± standard error value from 0, since a random selection of the habitat compositions should produce a mean of 0

TABLE 7.12: Percentage habitat composition within the minimum convex polygon (MCP) area of utilisation[1] estimate for toad number 92014 and within the total study area. The calculation of the difference between logratios is demonstrated, using the first column (the cultivated habitat) as denominator, for evaluation of habitat utilization.

	Cultivated	Improved	Rough	Wood	Hedge
Canopy	None	None	None	Open	None
Ground Cover	Poor	Yes	Yes	Yes	Yes
MCP area	0.243	0.050	0.385	0.307	0.015
Total area	0.246	0.249	0.267	0.198	0.040
Logratio (MCP)	-	-1.581	0.460	0.234	-2.785
Logratio (total)	-	0.012	0.082	-0.217	-1.816
Difference	-	-1.593	0.378	0.451	-0.969

TABLE 7.12b: Matrix of logratio differences between utilized and available habitat compositions for the toad 92014. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.593	-0.378	-0.451	0.969	
Improved	-1.593		-1.972	-2.044	-0.625	
Rough	0.378	1.972		-0.073	1.347	
Wood	0.451	2.044	0.073		1.419	
Hedge	-0.969	0.625	-1.347	-1.419		
Cultivated		+	-	-	+	3
Improved	-		-	-	-	5
Rough	+	+		-	+	2
Wood	+	+	+		+	1
Hedge	-	+	-	-		4

[1] Area of utilisation is used rather than home range in this study since toads were restricted within the test-enclosure and it was uncertain what influence this had on activity patterns.

TABLE 7.13b: Mean logratio differences between utilised and available habitat compositions for 12 female adult toads. Each mean is replaced by its sign, where mean differ significantly from 0, the sign is tripled. The number of positive values in each row ranks the corresponding habitat according to relative use; the most-used habitats have the highest ranks.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.222	-0.602	-0.392	-0.792	
Improved	0.222		-0.382	-0.168	0.587	
Rough	0.602	0.382		0.225	1.004	
Wood	0.392	0.168	-0.225		0.805	
Hedge	0.792	-0.587	-1.004			
Cultivated		-	-	-	-	5
Improved	+		-	-	+	3
Rough	+	+		+	+	1
Wood	+	+	-		+	2
Hedge	+	-	-	-		4

Habitat composition derived from radio-fixes versus MCP area of utilisation

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.032	0.373	0.917	0.975	
Improved	-0.032		0.225	0.719	0.945	
Rough	-0.373	-0.225		0.387	0.741	
Wood	-0.917	-0.719	-0.387		0.246	
Hedge	-0.975	-0.945	-0.741	-0.246		
Cultivated		+	+	+	+	1
Improved	-		+	+	+	2
Rough	-	-		+	+	3
Wood	-	-	-		+	4
Hedge	-	-	-	-		5

TABLE 7.13a: Magnitude of mean logratio differences between utilised and available habitat compositions for 9 male adult toads. Each mean is replaced by its sign, where mean differ significantly from 0 the sign is tripled. The number of positive values in each row ranks the corresponding habitat according to relative use; the most-used types have the highest ranks.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.580	-1.829	-1.937	-0.546	
Improved	-1.580		-0.247	-0.356	1.076	
Rough	1.829	0.247		-0.108	1.241	
Wood	1.937	0.356	0.108		1.391	
Hedge	0.546	-1.076	-1.241	-1.391		
Cultivated		+	-	-	- - -	5
Improved	-		- - -	-	+	5
Rough	+	+ + +		-	+	2
Wood	+	+	+		+++	1
Hedge	+ + +	-	-	- - -		5

Habitat composition derived from radio-fixes versus MCP area of utilisation

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-2.266	-1.507	-2.488	0.941	
Improved	2.266		0.959	-0.334	1.437	
Rough	1.507	-0.959		-1.296	2.449	
Wood	2.488	0.334	1.296		3.430	
Hedge	-0.941	-1.437	-2.449	-3.430		
Cultivated		-	-	- - -	+	4
Improved	+		+	-	+	2
Rough	+	-		- - -	+	3
Wood	+ + +	+	+ + +		+	1
Hedge	-	-	-	-		5

range, the habitat itself was not a vital part. Its inclusion in any MCP might therefore be by default as it was located in the centre of the enclosure.

7.2.4.5 Refugia

The location of day refugia selected by toads is shown in Tables 7.14a and 7.14b. In the enclosure at Coleorton toads were found at ground level at the base of long grasses, or in bushes, or underneath fallen logs or within mounds of rubble. Two animals were found to use small mammal burrows, one animal (021) used the stone wall that formed the eastern boundary of the enclosure. Other toads were found to use stones and breeze blocks that formed part of the perimeter fence.

At Osbaston Hall, toads in the Rookery could be found at ground layer at the base of the vegetation. In the arable fields (oil seed rape in 1994), toads were found to use nearby hedges and headlands or patches that were uncultivated or weed dominated. Toads were also found to exploit mammal holes and cracks in the ground, this was particularly noticeable in the arable field where there was little basal vegetation and plough scars and tractor wheel tracks were evident, Figure 7.3. The length of use of the refugia ranged from a single evening to periods of up to 14 days. Three toads tracked in the arable field were observed to leave their individual mammal hole, select a new day refugium less than 25m from the former refugium, then return to the original mammal hole. In contrast, ground level refugia were not observed to be used more than once. All toads that were lost to predation were those that took refuge within the arable field itself, no toads that used the field boundaries were predated, and there was no predation of radio-tracked toads in the Rookery.

7.2.5 Night searches

Osbaston was visited during the evenings of 44 days between days 162 and 244, as part of the radio-tracking studies. The number of toads seen on the road or during standard walks through each of the habitats was recorded and used as a rough indicator of toad activity.

7.2.6 Climatic cues for activity

Identifying the role of micro-climate in explaining toad activity was established as a

TABLE 7.14a: Characteristics of common toad refugia from the test enclosure, Coleorton and free-ranging animals at Osbaston Hall.

Refugia	Site	
	Coleorton	Osbaston
Logs or litter	5	8
Dense vegetation	31	38
Mammal holes	2	7
Other	15	7
TOTAL	53	60

TABLE 7.14b: Characteristics of common toad refugia tracked in released at Osbaston Hall 1994. Other refugia included cracks or ruts in the surface of the ground (Figure 7.3) common in the arable fields and the rubble from old farm buildings which existed on the edge of the rookery.

Refugia	Release Habitat, Osbaston Hall	
	Arable	Woodland
Logs or litter	5	3
Dense vegetation	19	19
Mammal holes	5	2
Other	6	1
TOTAL	35	25

Figure 7.3: Female toad using a crack in the arable field as a temporary refuge site, Osbaston Hall. June 1994.

TABLE 7.15: Measurements of activity from radio-tracking data for male and female toads, Test-enclosure, Coleorton. (* Large scale movements completed by two male toads having great influence on calculations, removing these values provides a mean rate of movement of 2.84 ± 1.07m).

Activity parameter	Males	Females
Mean total nightly distance moved m/evening ± SE (*n*)[1]	5.9 ± 5.2m* (124 toad-evenings)	4.9 ± 1.6m (140 toad-evenings)
Maximum observed movement[2] m/evening ± SE (*n*)	77.8 ± 72.4m (124 toad-evenings)	23.2 ± 3.3m (140 toad-evenings)
Activity index[3]	87.1% (55.6%)	79.3% (34.3%)

1:The total sum of toad evenings. 2: Maximum recorded nightly movement exhibited by individual toads. 3: Evenings where movement occurred or was observed as a percentage of the total number of evenings. The figure in parentheses represents the percentage of all nights where movement occurred greater than the mean rate of movement (the lower mean is used for the male).

TABLE 7.16: Measurements of activity from radio-tracking data for female free-ranging toads, Osbaston Hall.

Activity parameter	Arable	Rookery
Mean total nightly distance moved m/evening ± SE (*n*)[1]	10.8 ± 6.1m (143 toad/evenings)	13.1 ± 4.0m (124 toad/evenings)
Maximum observed movement[2] m/evening ± SE (*n*)	47.8 ± 17.9m (143 toad/evenings)	69 ± 16.8m (124 toad/evenings)
Activity index[3]	59.44% (34.96%)	69.32% (63.07%)

1:The total sum of toad evenings. 2: Maximum recorded nightly movement exhibited by individual toads. 3: Evenings where movement occurred or was observed as a percentage of the total number of evenings. The figure in parentheses represents the percentage of all nights where movement occurred greater than the mean rate of movement.

specific objective for the current study to provide a better understanding of habitat selection. The role of climatic conditions in explaining toad movements during spring has been addressed, by previous researchers (see references by Gittins *et al.*, Reading and Clarke and the data presented in Appendix 6), but despite this, it was considered appropriate to include analysis of the cues influencing summer activity to permit comparison with the spring and to help explain the observed activity patterns. The activity for the radio-tracked toads was quantified using three parameters: the maximum observed distance moved per evening; the mean distance moved per evening and the number of evenings where movement occurred this was expressed as a percentage of the total number of evenings over which the toads were tracked (after Tew 1992).

In the enclosure, males appeared to be more active, in terms of the mean distance, than the females (5.9 ± 5.2m per evening compared with 4.9 ± 1.6m), Table 7.15. The male result was heavily influenced by two individuals that escaped from the enclosure, these were removed the mean nightly distance moved was reduced to 2.84 ± 1.7m and the maximum distance was reduced to 16.8 ± 4.2m. These adjusted data were lower than for the females. Given this, females appear to be more wide ranging than males and this might explain why females showed wide use of all available habitats. The males were active on more evenings (87.1%), and a higher percentage of their forays were above the mean distance (55.6%) than the females (79.3%, 34.4%), Table 7.15.

For toads released at Osbaston, both the Arable (10.9 ± 6.2m) and Rookery (13.1 ± 4.0m) showed a higher mean nightly distance than the toads tracked in the enclosure (4.9 ± 1.6m). The female toads tracked at Osbaston were active on fewer evenings in the arable field (59.4%, 35.0%) than for the Rookery (69.3%, 63.1%), Table 7.16. The toads tracked in the Rookery also showed a higher mean nightly distance and a higher maximum distance than those released in the arable fields. The greater ground cover in the Rookery might have retained greater moisture and heat permitting activity on more evenings than in the arable fields. The greater risk of predation in the arable fields might reduce activity. Unfortunately, it is not possible to confirm these conclusions given the current study.

No significant correlations were shown for the 1992 climatic and activity data from the enclosure, although minimum temperature proved the strongest correlation, Table 7.17. At Osbaston Hall in 1994, maximum temperature ($p < 0.05$) minimum temperature ($p < 0.01$) and rainfall ($p < 0.05$) showed significant positive correlations with activity for the arable animals. That is to say, the high temperatures during the day, maintained during the evenings encouraged toad activity in the arable fields especially if it rained. The higher percentage of ground cover in the Rookery, and its ability to retain heat and moisture might reduce the importance of these variables. Wind speed showed a significant positive correlation with mean distance moved ($p < 0.05$) for the Rookery toads. For the Rookery, maximum temperature was negatively correlated with activity ($p < 0.01$), along with the number of sunshine hours ($p < 0.01$). Higher temperature during the day reducing the chances of activity in the Rookery.

The R^2-adjusted value found for multi-linear regression performed on all the climatic variables against activity patterns for both habitats at Osbaston was low explaining less than 27%, Table 7.18. The optimum subset of variables improved the R^2 value in both habitats but remained less than 35%. The models consisted of two universal variables *maxtemp* and *wind* with the addition of the variable *pressure* for the Rookery.

The number of toads seen active on any one evening in 1994 was not dependent upon any single climatic variable, Table 7.19. The highest correlation was observed for the minimum air temperature. The R^2-adjusted value for all the climatic variables against the number of toads seen active on a given evening was 22.1%. The variables with the greatest influence were *maxtemp, mintemp* and *sunshine hours*. This optimum subset increased the R^2-adjusted value to 23.3%; the high association of the individual variables made removal of any further variables less effective. The regression between the number of toads seen and the selected variables (*maximum and minimum temperature, sunshine hours and rainfall*) was significant ($F = 2.91$, $p<0.05$).

Principal component analysis was used to further analyze the activity patterns and climatic data. Table 7.20 shows the weighting for the first two principal components obtained from analysis in which all the climatic data were utilised ($n = 93$). These two

TABLE 7.17: Product moment correlations between number of toads seen outside the breeding season with recorded environmental variables, Osbaston Hall 1994. 1: Days measured since day 1, 1st January. NS not significant ($p > 0.05$). N = 27.

Climatic variable	r value	p value
Maxtemp	0.306	NS
Mintemp	0.356	NS
Rainfall	0.111	NS
Wind speed	-0.187	NS
Pressure	-0.242	NS
Sunshine hours	0.247	NS
Date [1]	-0.296	NS

TABLE 7.18: Comparison of R^2-adjusted values (in %) obtained in multi-linear regression between the number of toads seen and the mean evening distance moved in study habitats outside the breeding season, Osbaston Hall 1994.

	Number of toads seen	Mean distance moved - Rookery	Mean distance moved - Arable
Full set of climatic variables	22.1	26.2	16.1
Optimal subset *	23.3	34.1	20.7
* Optimal subset in descending order of significance	*Min* *Max* *Sunshine hours* *Rainfall* *Wind*	*Max* *Wind* *Pressure*	*Max* *Wind*

TABLE 7.19: Correlations (June - October) derived from the mean distance (m) moved during tracking and various recorded climatic variables, Coleorton 1992, Osbaston Hall 1994. * = p<0.05 ** = p<0.01

Climatic variable	Enclosure	Arable	Rookery
Maxtemp	-0.112	0.291*	-0.530**
Mintemp	0.239	0.352**	-0.225
Rainfall	0.252	0.266*	0.019
Wind speed	-0.062	0.239	0.371*
Pressure	-0.187	-0.335*	-0.263
Sunshine hours	-0.114	0.014	-0.336*

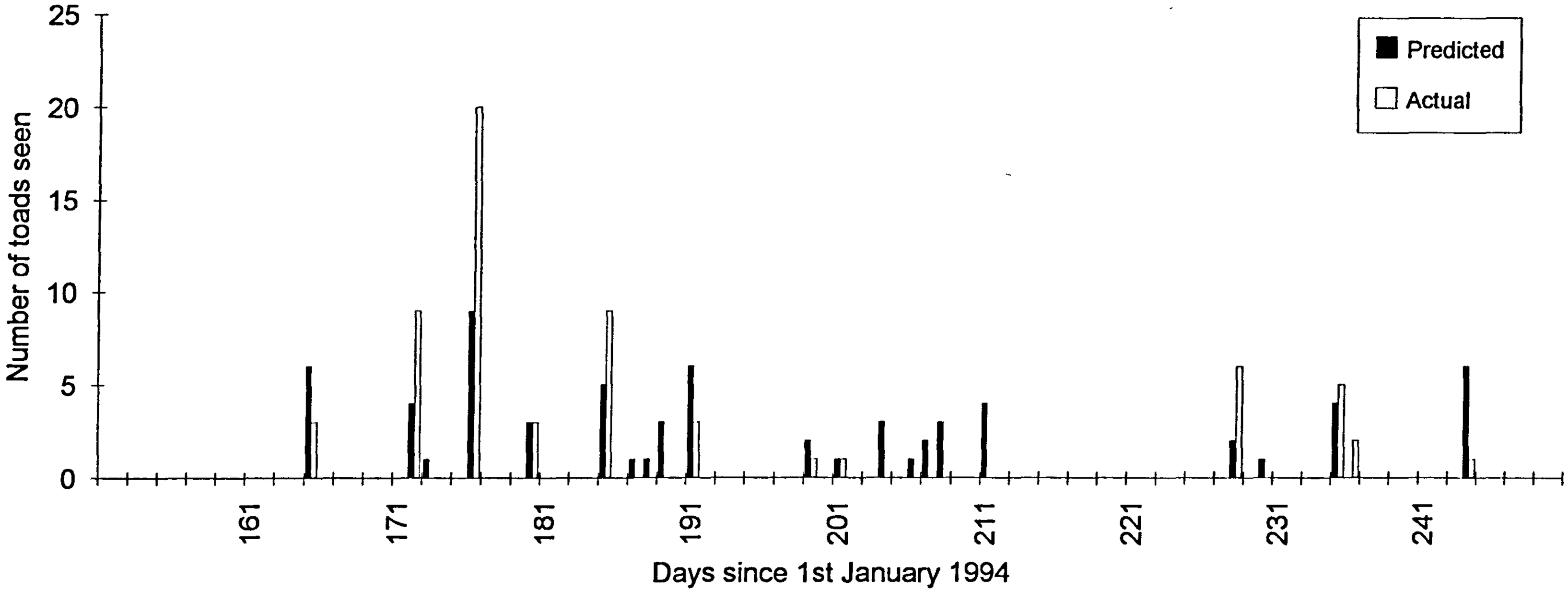
TABLE 7.20: Weighting of the three principal components (PC) in principal component analysis of climatic variables (n = 93) during summer 1994.

Climatic Variable	PC1	PC2
Maxtemp	0.529	0.436
Mintemp	0.638	0.042
Rain	0.288	-0.439
Wind	-0.273	-0.343
Pressure	-0.373	0.398
Sun hours	0.131	0.583

components accounted for 60.4% of the variance in the climatic data. The weighting for Component 1 was dominated by the temperature variables; *maxtemp* and *mintemp*. Component 2 again reflected temperature through *maxtemp*, but also *sunshine hours*, *wind speed* and *rainfall*. Activity may, therefore, be partly explained by the influence of day time temperatures and sunshine maintaining sufficiently high evening temperatures.

The regression statistic was used to predict the number of toads that could be expected to be seen given the weather conditions. This predicted number of toads was compared with the actual number of toads, Figure 7.4. The predicted and actual number of toads was significantly correlated ($r_s = 0.605$, $p<0.01$). Given the regression, 22 of the 44 evenings when visits were made, were considered suitable for toad activity. Despite this evidence from the actual observation indicated that the toads were active on fewer evenings, Figure 7.4. This may suggest that the sample technique was inefficient in recording toad activity, or may indicate that toads do not take advantage of all foraging opportunities.

Figure 7.4: Predicted and actual number of toads seen during night visits to Osbaston during the summer of 1994. The predicted number is calculated through regression analysis of the climatic factors believed to contribute to toad activity.



7.3 Discussion

7.3.1 Adult density

Adult density in woodlands was found to be between 4 and 12 times that observed in adjacent arable fields, Table 7.2. Analysis of the structure of the habitats suggests that the availability a high canopy layer is important in explaining habitat requirements for the adult toad, Table 7.1a and 7.1b. Within the general category of woodland, deciduous woodland appears to be of higher value than coniferous woodland, as shown by the data collected from Little Wittenham. This difference might be explained by the ground layer observed in deciduous woodland. Duff (1989) observed a significant correlation between adult density and the availability surface debris (ie leaf litter, logs etc) for the crested newt and similar material is used by toads for shelter and for over-wintering.

The estimated density for the woodland blocks at Osbaston Hall and Little Wittenham was higher than those provided for the common toad in other literature, Table 7.21. The estimates provided for the pasture habitat showed similarities to the studies by Gittins (1980), although were again higher than those suggested by Oldham and Swan (1991) and Honjanina (1953). The estimated density for arable habitats provided by Karg and Mazur (1969) was comparable with the figure estimated for Osbaston Hall.

The adult density estimated for the woodland blocks at both Osbaston and Little Wittenham showed distinct variation from year to year, while the density in the arable fields was more constant. This inter-year variation in the estimated density might result from a number of different reasons: for example the extrapolations required to calculate the estimates; a reflection of inter-year variation in habitat quality; an increase in predation within the habitats; or a possible fall in larval output, resulting in a fall in the recruitment of new animals. The method for calculating the adult densities was consistent throughout the study. Density was shown to be highly correlated with the structure of the vegetation, with higher densities occurring where habitats possessed both a dense ground layer and a tree canopy. There were no changes in woodland management over the period of the current study that could have reduced the suitability of the habitats to the toad. Within unaltered habitat it is unlikely that the

Table 7.21: Comparative densities for the common toad in contrasting habitats. 1: Data from woodland enclosure (1991-1992): Broadleaf woodland dominated by ash with understorey of bramble. 2: Data from the rookery enclosure (1991-1994): mixed woodland with exotic species and a tall herb and ruderal understorey. 3: Ash/hazel coppice with dog's mercury dominated understorey. 4: Pine plantation. 5: Rough grazing pasture. 6: Mixed agricultural landscape (unspecified). 7: Where a range is provided this is based on the data from several years of study. NK = Not known.

Study	Age	Habitat	Density
Honjanina (1953)	NK	Forest	100
This study (Osbaston)	Adult	Broadleaf [1]	200-500[7]
This study (Osbaston)	Adult	Mixed woodland[2]	200-600[7]
This study (Wittenham)	Adult	Mature coppice[3]	430 ± 110
This study (Wittenham)	Adult	Conifer plantation[4]	150 ± 54
Honjanina (1953)	NK	Orchard	70
Honjanina (1953)	NK	Garden	140
This study (Osbaston)	Adult	Rough pasture[5]	200-350[7]
Oldham and Swan (1991)	Adult	Mixed[6]	20
Gittins (1980)	Adult	Mixed[6]	350
Karg and Mazur (1969)	NK	Arable (root)	50
This study (Osbaston)	Adult	Arable (root)	50 - 70[7]
This study (Osbaston)	Adult	Arable (wheat)	20-60[7]
This study (Osbaston)	Adult	Arable (rape)	45
This study (Osbaston)	Adult	Arable (peas)	20

predation risk could have changed substantially over the study, unless there was an increase in predator pressure. The output of metamorphs from the ponds has, however, shown distinct variation (Chapter 6 and Chapter 8). These fluctuations in larval success are more likely to manifest themselves in variation in the adult population where habitats have a high carrying capacity, if it is assumed that the fluctuations are also below the carrying capacity of the terrestrial habitat. Where the carrying capacity of a terrestrial habitat is low, annual fluctuations in larval success may be less visible in the adult population since the population is restricted by the carrying capacity. The consistent adult density estimated for the arable areas suggests that these areas do have a lower carrying capacity and it appears that as long as the input of juveniles exceeds the carrying capacity in each year, any fluctuations in overall breeding output would not be carried into the observed adult density.

The toad density at Osbaston was higher in woodland blocks closer to the pond than those blocks in more distal locations (Poplars > Rookery > Spinney), Table 7.2. This pattern was not reflected at Little Wittenham, where a more homogeneous landscape existed and densities (as discussed for catches previously in Chapter 6) remained consistent throughout the woodland block, or even increased, Table 7.2b. As with Osbaston, toads over-wintered at distances in excess of 300m from the breeding pond at Little Wittenham. However, some toads overwintered at distances in excess of 300m, even where habitat considered favourable for over-wintering was available and not fragmented. The distal woodland blocks at Osbaston were isolated by arable fields; arable is considered to be less favourable for the toad than woodland and it may be more difficult for animals to disperse over less favourable habitat. It seems likely, therefore, that fragmentation of the landscape will reduce the density in quality habitats isolated by inferior habitats. Hedgerows may be used as refuge sites during migrations, however there is little cited evidence to suggest that adults use hedgerows as 'corridors' to and from core areas (i.e. breeding site, summer home range or over wintering site). Linking isolated woodland blocks with hedgerows will not reduce the problems of isolation, although such linear habitats are of value in their own right.

7.3.2 Habitat fidelity

Habitat fidelity appears to be an important force in shaping habitat use. For those toads using the Rookery and the Spinney habitats, between years fidelity was consistently estimated at over 80%. Fidelity to the Poplar's HSE habitat was lower, at less than 60%. Low fidelity for the Poplar's HSE might be explained through 'trespassing' from other habitats during migration to the pond and incorrect tagging; 34% percent of the toads caught and marked in Poplar's HSE in 1991 were recaptured in 1992 at the Spinney. It is quite possible that animals could evade the drift fence at the Spinney in 1991, and be caught at the Poplar's HSE. Their initial mark, indicating an origin from the Poplars, would therefore be incorrect. Migrants from other habitats pass through the Poplars towards the breeding site and could be intercepted by the Poplar fences.

In the Rookery and the Spinney habitats recaptures were almost exclusively from previous years' captures, Tables 7.4a - 7.4c. These traps were over 200 metres from the pond and were not adjacent to other traps, fence trespassing was therefore assumed to be low. This fidelity was maintained throughout the study, even where habitats appeared to be less favourable or required less favourable habitats to be crossed, despite the availability of more favourable habitats within a similar distance from the breeding site. The radio-tracking studies undertaken in the enclosure at Coleorton also indicated that familiarity with a habitat appeared more important, *per se*, than the habitat itself. One female (92010, Table 7.9) was caught in the cultivated section of the enclosure, tagged and was released and remained faithfully to that habitat despite the availability of the woodland and rough pasture habitats within 50m; evidence indicated that such a distance could be covered within 3-4 hours after release. Haapanen (1974) found that 50% of toads marked over a period of eight years were caught within 15 metres of the site where they had been caught previously, there was no marked difference in home range fidelity between young toads (ie less than 1 year old) and adult toads. This fidelity was apparent throughout the life of the animal, with one toad recaptured after 8 years only 14 metres from the site of its first capture.

This concept of high fidelity to former ranges has important implications when

considered in light of the hypothesis of larval fluctuations and adult density discussed in the previous section and the application of Fretwell's model (see Chapter 1, section 1.4.2), depicting a sequential infilling of habitats of lower suitability, starting with the 'best' habitats first. Fretwell (1972) indicates that when a population is high all habitats are used and the density of adults observed reflects the suitability. When total population falls the poorest habitats are not used and the population is based within the areas of prime habitat. This assumes that the most suitable habitats are always used to their optimum.

The data from Osbaston indicates that toads return to former habitats regardless of its 'suitability' and will remain faithfully to that habitat even if the an adjacent habitat, deemed more suitability, has spare capacity. High fidelity shows that habitats will be used regardless of suitability *per se*, and thus the better habitats are not always, therefore, used to their optimum. The previous section suggested that whilst the arable remained at its carrying capacity throughout the current study, the woodland areas did not. Familiarity to a habitat may have an impact on survival, since a 'safe' route to and from the breeding site and over-wintering areas will have been established. Franklin (1993) observed a similar tenacity to migration route to and from the pond for the great crested newt. A problem may occur, however, following significant changes in land management. Oldham and Swan (1991) report a decline over a number of years in the number of toads caught migrating towards the breeding site from a sector of the terrestrial habitat after agricultural improvement. This decline could be explained as a result of the loss of suitable habitat; with the carrying capacity of the habitat declining after agricultural improvement, the number of animals returning from each habitat to breed would reduce.

7.3.3 Summer activity patterns

Daytime temperatures and the warming and drying effect of the sunshine hours on the ground surface have a positive influence in explaining the number of toads active during any evening. Rainfall and wind speed were also considered to be important. Grist (1994) also showed significant correlations for the number toad captures with maximum and minimum temperatures and sunshine hours. These same correlations were of only moderate strength for the data collected in the current study, with none

showing a statistically significantly correlation with the number of toads seen active. Denton and Beebee (1992) found that the number of natterjack toads seen during summer nights increased with air temperature, with a threshold of 10° C required to encourage a foraging sortie. In addition, Denton and Beebee (1992) showed that rainfall was a particularly important influence on the activity patterns of the natterjack, with only a small amount of rain increasing the probability of toad sightings. The correlation between rainfall and toad sightings for Osbaston Hall was weak, and not significant ($r = 0.111$). On some occasions toads were not observed during night searches despite favourable conditions, Figure 7.4.

Females tracked in the arable field were active on less than 60% of the evenings on which tracking took place, Tables 7.16. Wide ranging movements. i.e. where the length (in metres) of movement was greater than the mean, occurred on less than 35% of the evenings. Oldham and Swan (1992) shown a similar pattern of periods of inactivity. Slater (1991) suggests a figure of only 11-22 warm wet evenings over the whole summer period would provide sufficient periods of activity for a toad to accumulate sufficient reserves for the winter. This assumes that foraging does not occur during sedentary periods. Given evidence to suggest that the common toad may be considered a 'sit-and-wait' predators (Larsen 1984), foraging from its refugium is certainly possible. In addition, data from stomach flushing of toads caught during night searches indicates a regular input of food items (Oldham pers. comm.). Although there is evidence to suggest that toads do not leave their refugia on every suitable evening, the estimate of 11-22 is likely to be a under estimate of actual foraging patterns over the terrestrial season.

Despite the available cover in the arable fields from the oil seed rape crop, all the cases of predation in 1994 were observed within the crop itself during late June. Those animals that were tracked at the same time, but used the field boundaries and headlands were not predated. Despite attempts to study the utilisation of the arable fields after harvesting during the current study, data from too few animals were collected for meaningful results. The limited data that were available suggested that toads in newly harvested fields were less active than prior to harvesting, with three tracked individuals remaining unmoved over a two-week period. Tew (1992) noted a

greater utilisation of arable fields by radio-tracked woodmice once the crop had grown sufficiently to provide satisfactory cover against predation, and during this period the arable fields were used over and above the woodland and hedge habitats. However, after, harvesting an increase in aerial predation and emigration from the arable fields back to surrounding woodlands, decreased the population by 80%. The process of harvesting itself had little impact on the mice, with only 1 out of 33 mice killed by the combine harvester (3%). However, 17 of 32 (53%) disappeared within one week of harvest (Tew and Macdonald 1993) due to the previously mentioned reasons.

In a controlled situation where four contrasting habitats were available to the toad, selection of the woodland was higher than the remaining habitats, although individuals were observed to utilise the cultivated and improved grassland. In free-ranging animals arable fields were again used, although predation was shown as a clear risk to those individuals that did not take cover in headlands and hedges. It could be assumed that the increase the use of the arable fields was probably linked to when the crop had grown sufficiently to provide cover, in addition it is likely that this would be associated with an increase in the availability of carabid beetles, a major food source of arable toads (Cornish pers. comm.).

Free-ranging animals released into woodland were more active than their arable counter-parts, but did not respond to climatic influences in the same manner as the more exposed arable animals. High temperatures during the day, that maintained a warm evening temperature encouraged toad activity in the arable fields, especially if it rained. Activity for radio-tracked toads released into the Rookery was reduced if daytime temperatures where high ($p < 0.01$), only wind speed showed a significant (+ ve) correlation with mean distance moved ($p < 0.05$).

7.3.4 Home ranges

The home ranges observed by the free-ranging females were significantly larger than for the enclosure, which might indicate that the movements were indeed restricted by the enclosure. The Rookery animals were more active than the arable animals and illustrated a larger home range. The home ranges were again highly variable, although less variable in the Rookery than in the arable fields. There was no

significant difference between the two habitat types. At Little Wittenham, the home-range calculated for a toad using coniferous woodland (admittedly based on only one individual) was 3 times larger than the range for toads using the deciduous woodland.

There are few other studies that describe the size and nature of the home range of the common toad; Haapanen (1970) described the home ranges of common toads in southern Finland as 59m^2, far smaller than those recorded by Sinsch (1987) and Denton and Beebee (1993a), Table 7.22. The home range estimates by Denton and Beebee (1993a) were undertaken through radio-tracking and by Sinsch (1987) through a mechanical trailing device, used the minimum convex polygon (see Kenward 1989), comparable with the methods used for the home ranges of toads tracked at Osbaston Hall. The home ranges observed during the current study are notably higher than those calculated by Sinsch (1987), but more comparable with those estimated by Denton and Beebee (1993a). The home-ranges at Little Wittenham were comparable with Haapanen (1970).

The mean home ranges calculated for the Rookery and with the arable fields are likely to be influenced by the limited number of toads used to estimate the ranges (n = 12) and that large scale movements may exaggerate the size and the shape of the home range. Also, since the majority of the toads used in the tracking studies were collected during the spring migration, it is possible that the toads were intercepted within a habitat where they had not originated. This might be particularly true for toads caught and released as arable toads. These animals were caught at Arable West (AW) and at the arable/arable hedge (HAO A-C). The estimate of the home range for the 'new' habitat may thus be invalid, due to the tenacity of the individual and its homing behaviour. Difficulties were also observed when some animals did not move for 2 weeks during tracking.

It is interesting to note that the maximum distances moved on toads on successive night (Tables 7.15 and 7.16) were less than 80m, and that movements were believed to be based around a central location. Given this, the selection of method similar to the mechanical trailing device described by Dole and (1965) Sinsch (1987) might have been as appropriate, and certainly more cost-effective, as the radio-tracking.

TABLE 7.22: Comparison of summer home range size in the common toad in contrasting habitat types. All home ranges are calculated using the convex polygon method where stated. 1: Home range expressed in m^2. 2: After Loman (1994). 3: Both females and males. 3: Females only. 4: Based upon the minimum area of a circle encompassing all catch sites.

Study	Age	N	Habitat	Home range [1]
Haapanen (1970)[2]	Adult	29	Not stated	59
Sinsch (1987)	Adult	23	Pine forest, pasture	1901 ± 312
Denton and Beebee (1993)	Adult	3	Lowland heath	3818 ± 1033
Denton and Beebee (1993)	Adult	1	Dune scub	1988
This study	Adult [3]	12	Arable	4161 ± 3064
This study	Adult [3]	12	Mixed Woodland	5602 ± 1472
This study (LWNR) [4]	Adult	1	Coniferous woodland	1500
This study (LWNR) [4]	Adult	3	Deciduous woodland	300

7.3.5 Use of habitat features and small scale elements

Those common toads that were followed using radio-tracking illustrated a preference for surface refugia with over 90% of the refuge sites located above ground, Tables 7.14a-7.14b. Although there may be some bias in this estimate, since these animals were disturbed more than would be expected. Previous studies (Denton and Beebee 1993b) have shown a similar preference for surface refugia during the summer, where individuals were found to utilise surface debris such as logs and leaf litter. It is unlikely that a common toad could create its own hollow in the substrate at Osbaston Hall or Coleorton and other studies suggest that common toads do not burrow (Denton and Beebee 1993b), thus it was assumed that where toads were found buried the burrow had been created by a small mammal.

The selection of surface refugia by the common toad has important implications for predation. During the current study five out of twelve toads were lost to predators in the arable fields at Osbaston, one further toad was predated by a magpie in the enclosure at Coleorton, but no toads were lost in the Rookery, Osbaston. Denton and Beebee (1993a) lost three out of eight common toads to grass snakes at a lowland heath in southern England. Toads formed nearly 75% of prey in a study of grass snake ecology in Hampshire, England (Brown 1991) and grass snakes were seen raiding pitfall traps at Little Wittenham (Franklin pers. comm. and pers. observation). Surface refugia in the open habitats, such as the arable fields, may be more accessible to predators. All the toads tracked in the current study were adults. Juvenile toads might be able to exploit smaller habitat features. Cornish (pers. comm.) found that slate roofing tiles used as the artificial and placed in terrestrial habitats were used mainly by juvenile toads under 25mm (tip of snout to urostyle dorsal length). These tiles (1500cm^2) might have been too small for adults or their rigidity might hamper their use. Denton and Beebee (1993b) found that artificial refugia were also used infrequently by adult common toads.

The inclusion of refugia in the assessment of habitat quality for toads needs to be considered in light of the overall structure of the habitat. In open habitats where there is limited basal vegetation, for example an arable field, the presence of refugia may be critical and their value higher than in habitats like the woodland where there is a

thicker dense ground layer combined with natural log piles forming hiding places. The population density of the frog *Eleutherodactylus coqui* was, in part, regulated by the availability of refuge sites in the Luquillo forest, Puerto Rico (Stewart and Pough 1983), frogs unable to find suitable refuge were found to be under increased pressure from predation.

Chapter Eight: Population dynamics of the common toad

8.1 Introduction

The study of the common toad population at Osbaston Hall was divided according to three life-stages; larval development up to metamorphosis, post-metamorphosis and juvenile; and the adult stage. The dynamics of the population were investigated using data collected during the breeding season, and the exodus of metamorphs later in the year. The data from these studies have been reported in Chapter 6. The overall aim for this chapter is to determine the size and magnitude of any inter-year variation in adult population size that may occur in terms of habitat utilisation. There were three specific objectives; first to identify the stage of the toad's life cycle stages that had the greatest influence on the population regulation, or variation in population characteristics. Secondly, to establish the variation in growth during the three stages of the toad's life-history and how these are affected by habitat use and third; by sampling a single population it was hoped that the consequences (or impact) of the use of specific habitats may be evaluated through defined ecological parameters in order to compare the suitability of habitats for the common toad.

8.2 Results

8.2.1 Larval development up to metamorphosis

Larval development has not been studied in detail in the current study and research has been concentrated on the life-history of the toad post-metamorphosis. Metamorphs were stored in formaldehyde on collection from the traps and weighed and measured in laboratory at a later date. Metamorphs were caught and classed as belonging to each of the six development classes[1]. The percentage of the metamorphs retaining some evidence of their tail provides an indication of the time since emergence since final absorbtion occurs during the first few days on dry land (Oldham pers. comm.).

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[1] 5-1, with declining amounts of tail, and Stage 0 representing metamorphs with total tail absorption. As detailed in methods

8.2.1.1 Spatial variation in mass at emergence

In 1991, metamorphs emerging from Lake West (LW) were smaller than those from Lake North (LN) (0.137 +/- 0.006g compared to 0.302 +/- 0.020g, Mann-Whitney U-test $p < 0.05$) however, the small sample size might have influenced this result, increasing the standard error observed for both Lake South (LS) and LN, Table 8.1.

In 1992, 80% of the Lake metamorphs emerged on LW. Seventy-five percent of the metamorphs were classed as either Stage 1 or Stage 0. Since the final stages of tail absorption occurs post-emergence, this suggests that the early part of the temporal emergence period was missed, as noted in Chapter 6. Metamorphs emerging from LW were significantly smaller than those from LN, LS and LE (ANOVA, $F_3 = 99.74$, $p < 0.01$), Table 8.2. There was no significant difference, however, between the mean mass of the metamorphs emerging from LS, LN and LE (ANOVA, $F_2 = 1.46$, $p = 0.235$). Metamorphs from the Spur were significantly larger than those from any part of the Lake (ANOVA, $F_4 = 104.00$, $p < 0.01$), Table 8.2.

Since the largest emergence was on LW these metamorphs were analyzed separately. There was no significant difference between metamorphs caught in the traps on LW falling into classes 1 to 5 (ANOVA, $F_3 = 0.16$, $p = 0.925$), i.e. retaining some evidence of a tail. However, those classified as Stage 0 were significantly larger than the combined group of metamorphs with some remaining tail ($F_1 = 20.58$, $F < 0.01$), Table 8.3a.

Metamorphs at Stage 0, the most numerous group from all the banks were also analyzed separately. The samples from different banks of the Lake at Stage 0 were significantly different (ANOVA, $F_3 = 68.75$, $p < 0.01$), and as with the combined sample, the smallest animals emerged from LW, Table 8.3b.

Tukey test results are provided in Appendix 9.

In 1993, 20% of the total gross catch from the Lake were classed Stage 0, with less than 5% classed as Stage 5. The highest number of metamorphs again emerged from LW. There was no significant difference between the mass of metamorphs

TABLE 8.1: Mean mass (g) at emergence of metamorphs from the breeding site at Osbaston, summer 1991. There was a significant difference between lake north and lake west (Mann-Whitney tests U-test, $p < 0.05$)

Side	n	Mean (± SE)	Median
Lake North	22	0.302 ± 0.020	0.302
Lake South	3	0.206 ± 0.012	0.207
Lake West	170	0.137 ± 0.006	0.130
Lake East	sample lost		
Spur			

TABLE 8.2: Mean mass (g) at emergence of metamorphs the breeding site, Osbaston, 1992. There was no significant difference between between the masses of metamorphs emerging from the north, south or east side of the lake (ANOVA). Metamorphs from the west side of the lake were significantly smaller (ANOVA, $F_1 = 99.74$, $p < 0.01$) than those from Lake North, South or East. Metamorphs emerging from the spur were significantly larger than those from the lake (ANOVA $F_1 = 104.00$, $p < 0.01$)

Side	n	Mean (± SE)	Median
Lake North	103	0.154 ± 0.005	0.139
Lake South	32	0.142 ± 0.007	0.136
Lake East	115	0.158 ± 0.004	0.151
Lake West	576	0.115 ± 0.001	0.112
Spur (Total)	57	0.185 ± 0.008	0.183

TABLE 8.3a: Mean mass (g) at emergence of metamorphs from the Lake West only at Osbaston, summer 1992. The sample has been divided into the six development stage, based on tail absorption. There was no significant difference between the mean mass at each development stages 1-4 (ANOVA, $F_3 = 0.16$, $p = 0.925$), however metamorphs at development stage 0 were significant larger than the combined sample from the other stages (ANOVA, $F_1 = 20.58$, $p < 0.01$)

Stage	n	Mean (± SE)	Median
0	397	0.119 ± 0.001	0.117
1	147	0.110 ± 0.001	0.109
2	15	0.109 ± 0.004	0.100
3	17	0.112 ± 0.003	0.111
4	3	0.106 ± 0.009	0.111
5	No samples		

Stages:
5 tail visible and unabsorbed
4 tail visible (some reabsorption)
3 extended stump
2 stump
1 small stump
0 complete reabsorption.

TABLE 8.3b: Mean mass (g) at emergence of metamorphs at development stage 0, Osbaston, 1992. The samples from different banks of the Lake were significantly different (ANOVA $F_3 = 68.75$, $p < 0.01$).

Side	n	Mean (± SE)	Median
Lake North	93	0.155 ± 0.005	0.155
Lake South	28	0.141 ± 0.007	0.141
Lake East	101	0.161 ± 0.004	0.161
Lake West	397	0.118 ± 0.001	0.118

TABLE 8.4: Mean mass (g) at emergence of metamorphs from the breeding ponds at Osbaston, 1993. There was no significant difference between the masses of metamorphs emerging each of the sides of the lake when compared collectively (ANOVA $F_3 = 2.08$, $p > 0.05$), however those metamorphs from lake west metamorphs were significantly smaller than those from lake east (Mann-Whitney U-test, $p < 0.05$). The metamorphs from spur were larger than those from the lake (Mann-Whitney U-test, $p < 0.01$)

Side	n	Mean (± SE)	Median
Lake North	45	0.222 ± 0.007	0.220
Lake South	51	0.214 ± 0.009	0.214
Lake East	26	0.224 ± 0.005	0.223
Lake West	935	0.209 ± 0.001	0.209
Spur (Total)	13	0.292 ± 0.070	0.292

emerging from the different sides of the Lake (ANOVA, $F_3 = 2.08$, $p = 0.101$) during the full emergence period, when all four sides were analyzed as a group. However, the LW metamorphs were significantly smaller (Mann-Whitney, U-test, $p < 0.05$) than the LE, Table 8.4. There was no significant difference between the mass of metamorphs at the different development stages (ANOVA, $F_5 = 0.91$, $p = 0.471$) for the whole Lake sample, Table 8.5a. When analyzed separately, despite a trend in the data indicating a decline in the mean mass with tail absorbtion, there was no significant difference in the mass of metamorphs at different development stages for the LW sample (ANOVA, $F_5 = 1.72$, $p = 0.129$), Table 8.5b.

Emergence from the Spur was low in 1992, providing a sample of only 13 animals for analysis, however the Spur metamorphs had a significantly higher mass (Mann-Whitney, U-test, $p < 0.01$) than those from the Lake sample consisting of LN, LS and LE (LW had been removed because it was significantly different from LE). Removal of two large metamorphs from the sample, caught during the last few sample days around the Spur, did not change the statistical significance of test.

In 1994, both the Lake and the Spur appeared to suffer a mass mortality of tadpoles prior to metamorphosis, and emergence was very low. A total of only 20 metamorphs was caught emerging from the Lake and only three metamorphs from the Spur. The low sample size meant that only LN and LW could be compared. The mass at emergence of these two groups was not significantly different (Mann-Whitney, U-test, $p > 0.05$), Table 8.6.

Significant variation occurred between the metamorphs emerging from the different banks of the Lake in 1991, 1992 and 1993 (although the significant variation only occurred between LE and LW when analyzed separately), Table 8.7. In each of the years 1991-1993, LW metamorphs were smaller than those from other banks. The greatest number of metamorphs emerged from LW. The smaller size of the LW metamorphs, given their greater numbers might indicate some form of competitive stress. However, the greatest output of metamorphs was estimated in 1993, when a consistently high mass at emergence was recorded for each of the Lake banks, Table 8.8. Smith (1987) showed for the chorus frog (*Pseudacris triseriata*) that resource

TABLE 8.5a: Mean mass (g) at emergence of metamorphs from the Lake at Osbaston, summer 1993. The sample has been divided into the six development stage, based on tail absorption. There was no significant difference between the mean mass at each development stage (ANOVA, $F_5 = 0.91$, $p = 0.471$)

Stage	n	Mean (± SE)	Median
0	168	0.212 ± 0.005	0.209
1	86	0.215 ± 0.004	0.218
2	50	0.207 ± 0.004	0.202
3	47	0.201 ± 0.005	0.202
4	38	0.201 ± 0.005	0.209
5	26	0.221 ± 0.007	0.213

TABLE 8.5b: Mean mass (g) at emergence of metamorphs from LW at Osbaston, summer 1993. The LW sample has been divided into the six development stage, based on tail absorption. There was no significant difference between the mean mass at each development stage (ANOVA, $F_5 = 1.72$, $p = 0.129$)

Stage	n	Mean (± SE)	Median
0	77	0.200 ± 0.007	0.190
1	68	0.214 ± 0.005	0.212
2	45	0.206 ± 0.005	0.201
3	40	0.201 ± 0.004	0.201
4	35	0.208 ± 0.005	0.205
5	26	0.221 ± 0.007	0.213

Stages:
5 tail visible and unabsorbed
4 tail visible (some reabsorption)
3 extended stump
2 stump
1 small stump
0 complete reabsorption.

TABLE 8.6: Comparative size (g) of metamorph from the lake at Osbaston, summer 1994. The mass of LN and LW was not significantly different (Mann-Whitney, U-test, p >0.05).

Side	n	Mean (± SE)	Median
Lake North	9	0.155 ± 0.024	0.140
Lake South	1	0.171	0.171
Lake East	2	0.187 ± 0.024	0.187
Lake West	8	0.182 ± 0.020	0.173
Spur (Total)	3	0.377 ± 0.077	0.431

TABLE: 8.7: Comparative size (g) at emergence for metamorphs from the breeding ponds at Osbaston, 1991-1994. There was a significant difference between the mass at emergence for metamorphs emerging from the lake (ANOVA $F_3 = 656.69$, $p < 0.01$)

	Mean mass (± SE) of toadlet at emergence (g)			
	1991	**1992**	**1993**	**1994**
Lake North	0.302 ± 0.020	0.154 ± 0.005	0.222 ± 0.007	0.155 ± 0.024
Lake South	0.206 ± 0.006	0.142 ± 0.007	0.214 ± 0.009	0.171 ± 0.000
Lake East	sample lost	0.158 ± 0.004	0.224 ± 0.005	0.187 ± 0.024
Lake West	0.137 ± 0.006	0.115 ± 0.001	0.209 ± 0.001	0.182 ± 0.020
Whole Lake	0.164 ± 0.006	0.127 ± 0.001	0.210 ± 0.001	0.169 ± 0.013
Spur	sample lost	0.185 ± 0.008	0.292 ± 0.070	0.377 ± 0.077

TABLE 8.8: Output of metamorphs at Osbaston Hall from both the Lake and Spur during 1991-1994

Year	Spur	Lake
1991	400	14,000 ± 170
1992	4000 ± 170	136,000 ± 4,000
1993	1500 ± 90	220,000 ± 10,000
1994	combined output < 2000	

availability within the aquatic stage had a lasting influence on the species into the terrestrial stage, with small metamorphs becoming small adults. Cummins (1989) made similar conclusions for the dynamics of the common frog. The smaller metamorphs emerging from LW at Osbaston would, therefore be considered to be disadvantaged, and the size variation maintained throughout the life-history of the individual.

The output from both the Lake and Spur was consistently low, and variable from year to year. The mean mass of the metamorphs emerging from the Spur was, however, higher than those from any part of the Lake. The small size of the sample from each of the sides of the Spur did not permit internal comparison. Spur masses did show variation between the years, with significant variation between 1992 and 1993 (Mann-Whitney, U-test, $p < 0.01$). The mass at emergence of metamorphs caught at the Spur appeared to increased during the period 1992-94, Table 8.7.

8.2.1.2 Temporal variation of mass at emergence

Despite sampling throughout 1991-1994, only in 1992 and 1993 did a sufficiently large number of metamorphs emerge from the Lake to provide an opportunity to study the variation in metamorph size during emergence. In 1992 the start of the emergence was missed and thus, only in 1993 was the data set considered to be complete. In 1993, emergence was characterised by an increase in metamorph mass during its mid-part. The pattern was clearest where emergence was highest, i.e. LW, but also occurred on LN, Figures 8.1 and 8.2.

One way analysis of variance conducted on the data set representing the early, mid and late emergence for LW in 1993, showed significant variation in mass (ANOVA, $F_2 = 208.28$, $p < 0.01$), Table 8.9. An increase in the mass of metamorphs during the middle part of the emergence period was also evident in 1992 for LW, Figure 8.3, although the variation in mass at emergence was attributable to the difference between those emerging early in the period and those during the late part of emergence (ANOVA, $F_2 = 6.68$, $p < 0.01$). The 1992 data are questionable given the previously mentioned omissions.

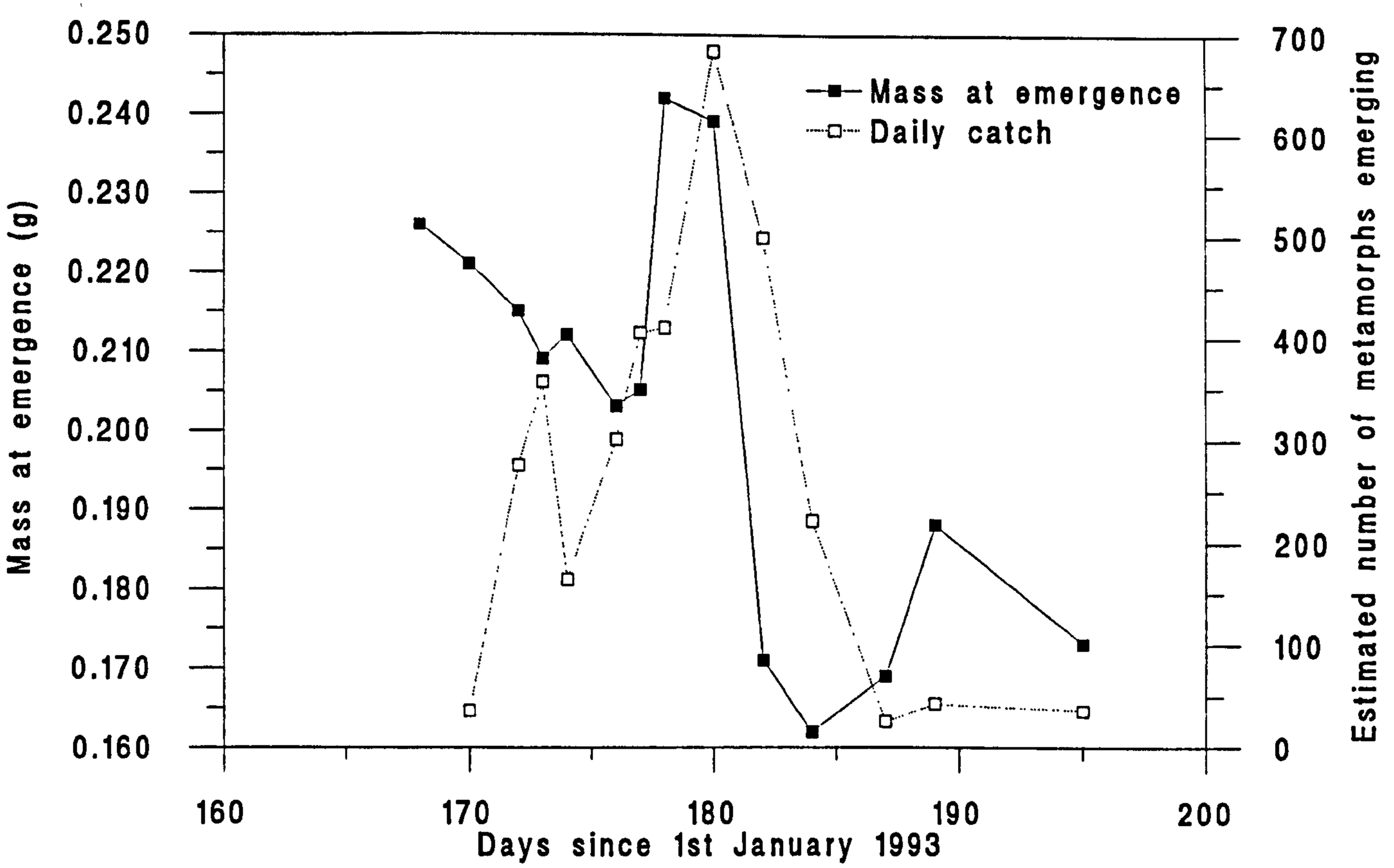

Figure 8.1: Mean mass (with standard errors) and numbers emergening from the western bank of the lake at Osbaston Hall during 1993

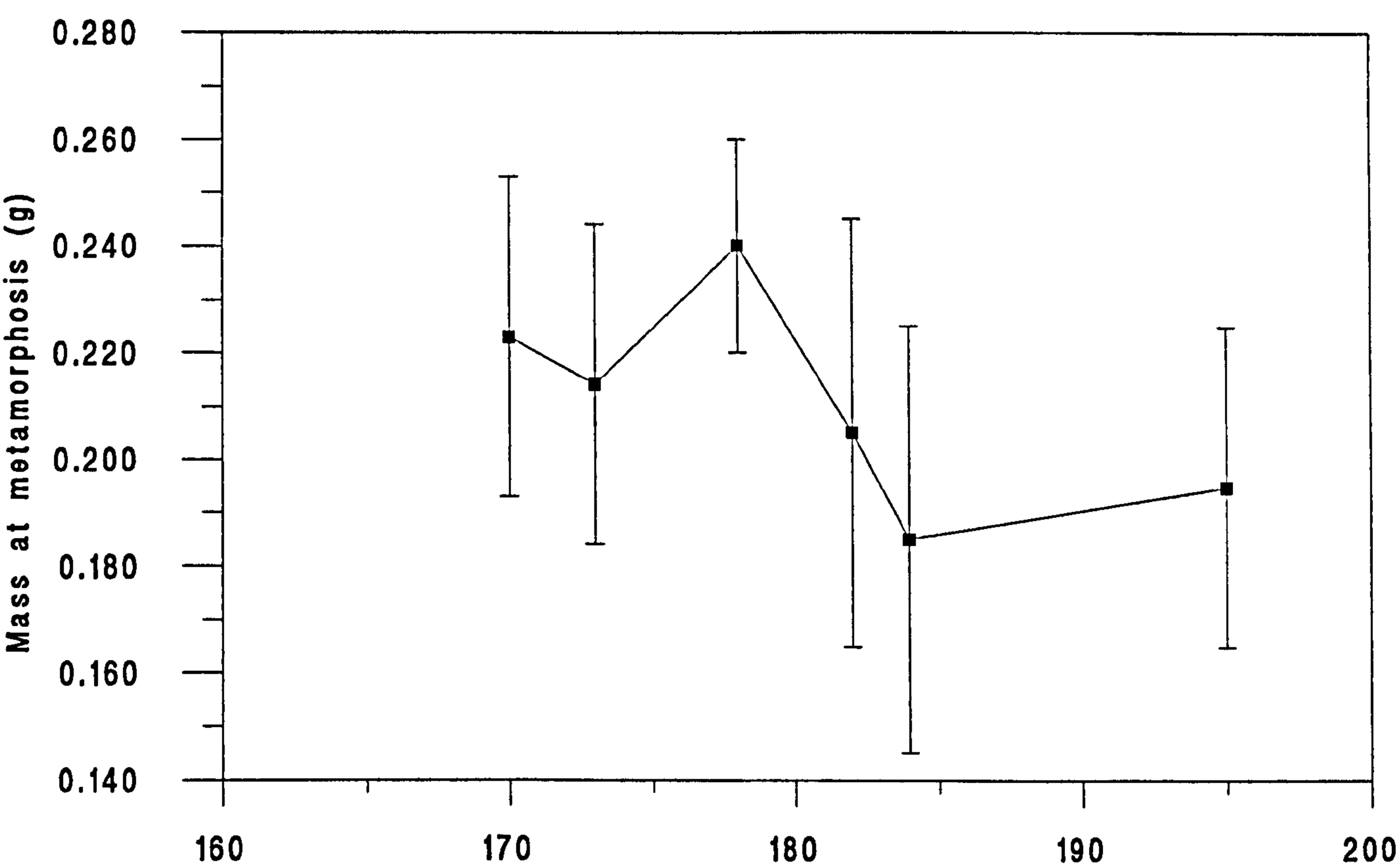

Figure 8.2: Mean mass at metamorphosis (with standard errors) of toadlets during emergence from the northern side of the lake, Osbaston 1993.

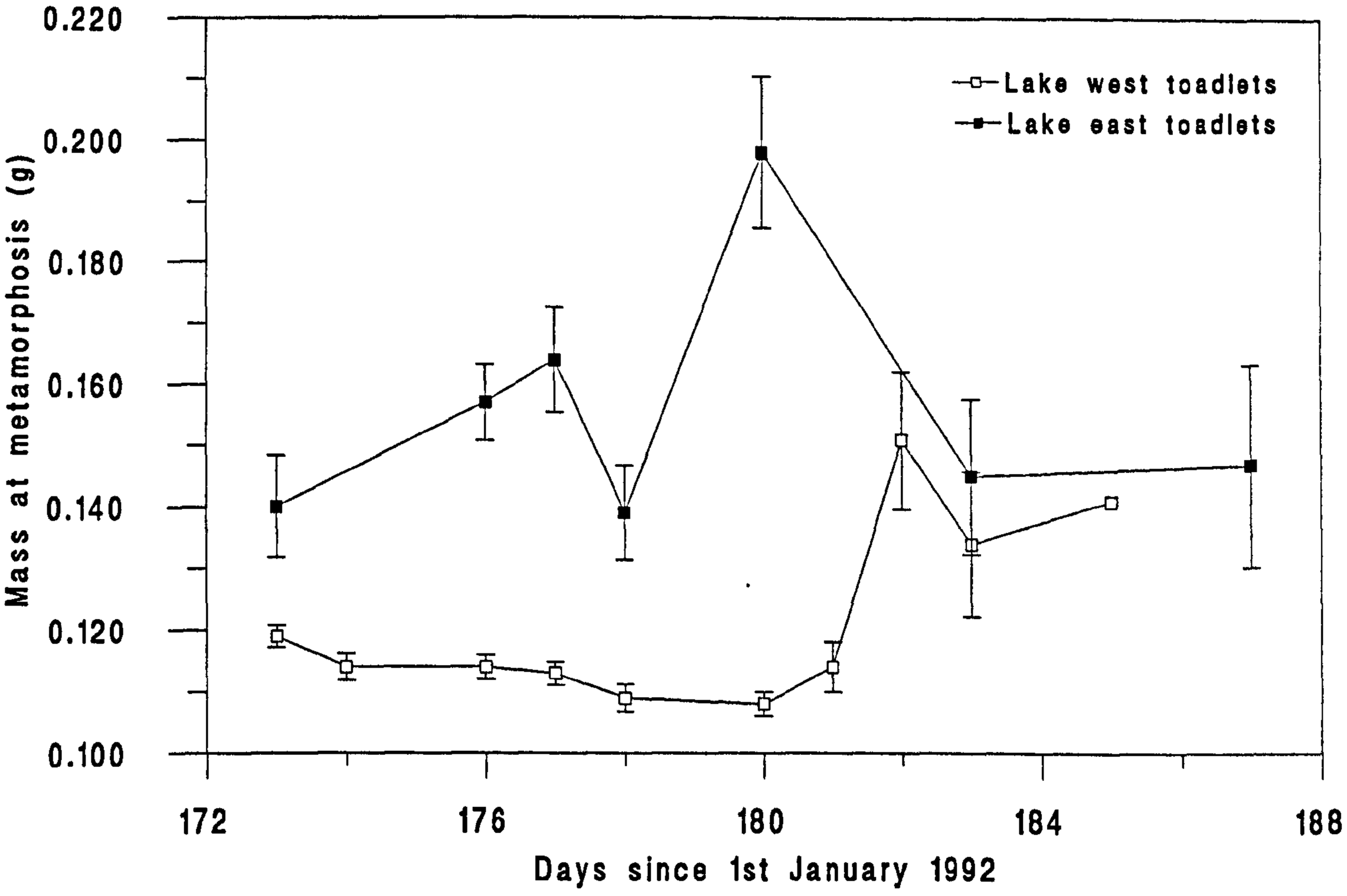

Figure 8.3: Mean mass at metamorphosis (with standard errors) of toadlets from the eastern and western side of the lake over period of emergence, Osbaston 1992.

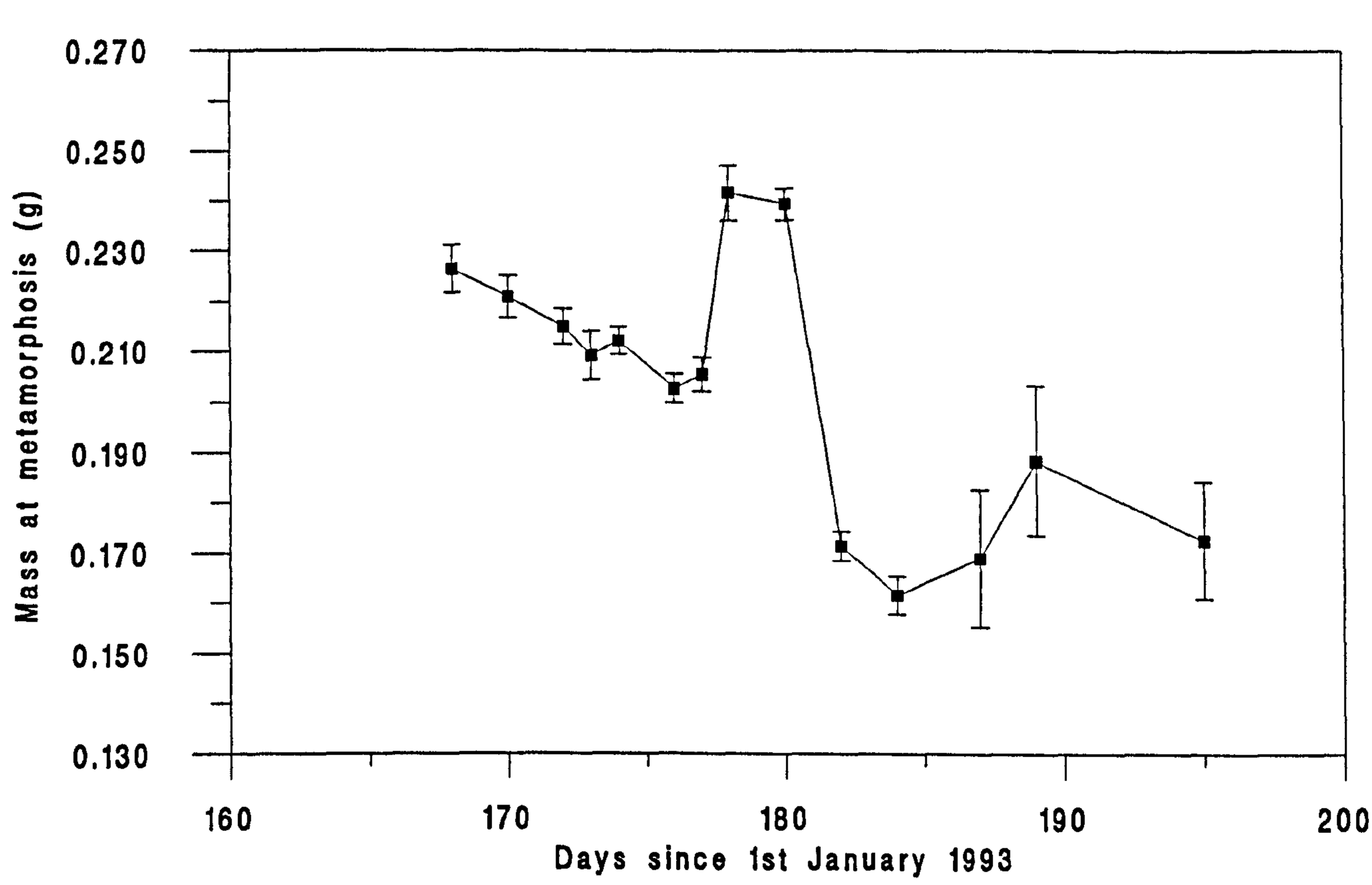

Figure 8.4: Mean mass at metamorphosis (with standard errors) of toadlets during emergence from the western side of the lake, Osbaston 1993.

Metamorph mass reached a maximum during peak emergence, although there was general downward trend in mass, Figure 8.4. The percentage of the sample retaining some of its tail declined during the sampling period, as the mean mass increased, Figure 8.5. Newly emerged metamorphs remain close to the edge of the pond after leaving the water (Oldham pers. comm.), and full tail absorption is completed on land, therefore those individuals caught later in the season, with clear evidence of tail re-absorption, may have left the pond earlier than their catch date indicated and gained some benefit from terrestrial foraging. However, in 1993 there was no significant difference between the mean mass of metamorphs at any of the different development stages and animals are not believed to feed on land during the first few days post-emergence.

8.2.2 Post-metamorphosis and juvenile stage

8.2.2.1 Post-metamorphosis dispersal and growth

The speed of movement by the metamorphs at Osbaston in 1993 was estimated as an average of 5m/day across a wheat field during July-August when the crop was fully grown. This calculation assumes that the animals moved in a straight line after emergence (Oldham and Swan 1991).

The mean mass of metamorphs emerging from the western side of the Lake during 1993 was 0.209 ± 0.001g, Table 8.9. The mean mass of metamorphs caught in the metamorph traps in the arable field to the west of the breeding site, 100m from the pond was 0.290 ± 0.04g and 0.313 ± 0.011g at the Spinney, 400m from the pond. The first catch at the Arable West was 32 days after first metamorph catches and 58 days at the Spinney. This represents a growth rate of about 0.005g per day.

Mean body-length at metamorphosis in 1993 was 11.4 ± 0.1mm, Table 8.10. There was no significant difference between the body-lengths[2] of metamorphs emerging from each of the banks (ANOVA, F_3 = 1.1.8, p = 0.317). Length at emergence may be

[2] At emergence ossification of bones would not have occurred, therefore measurements may be in accurate and lengths should be treated with some caution. Ossification would occur over the first wintering period.

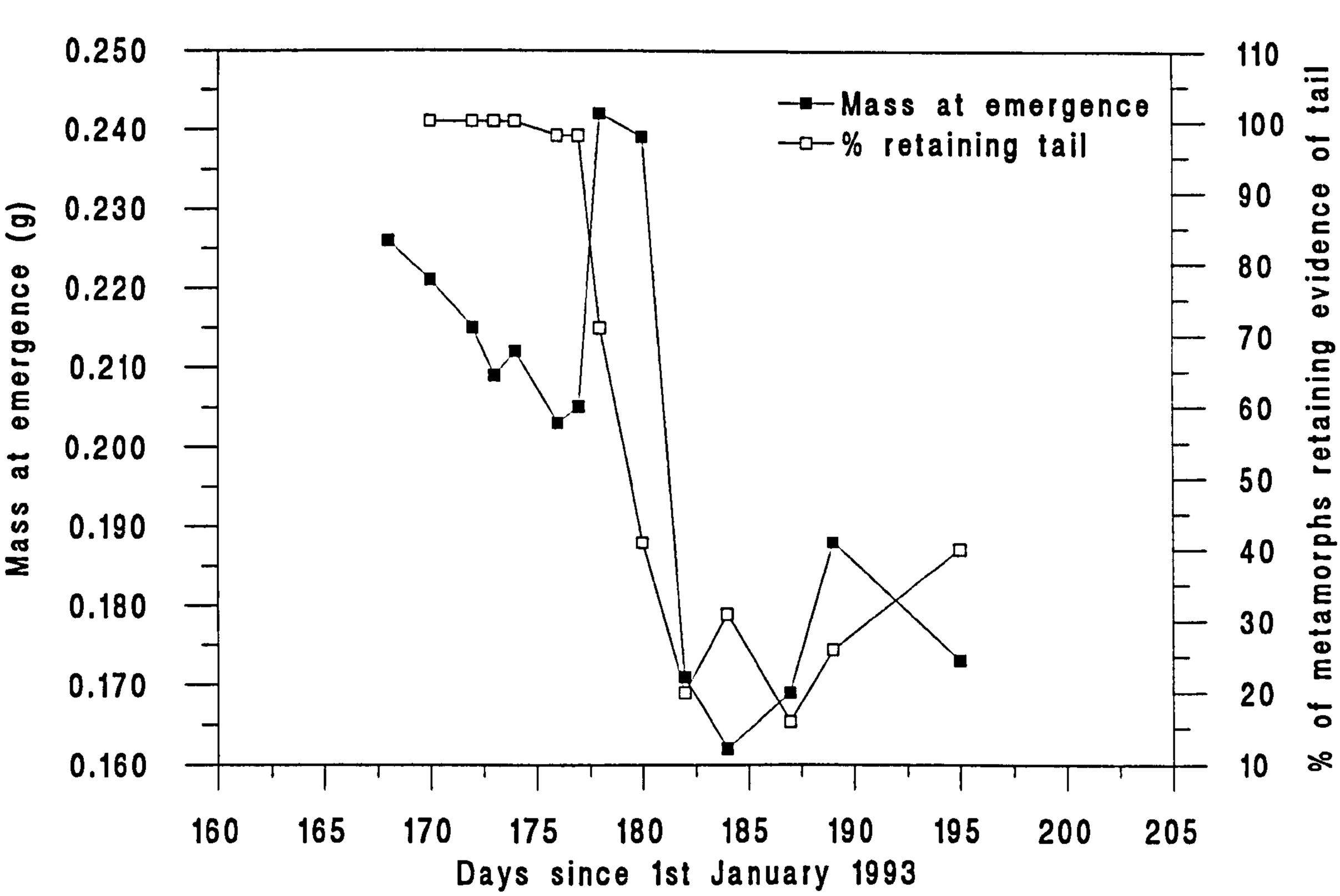

Figure 8.5: Variation in mass and percentage of sample retaining some tail, for metamorphs caught on Lake West, Osbaston Hall 1993.

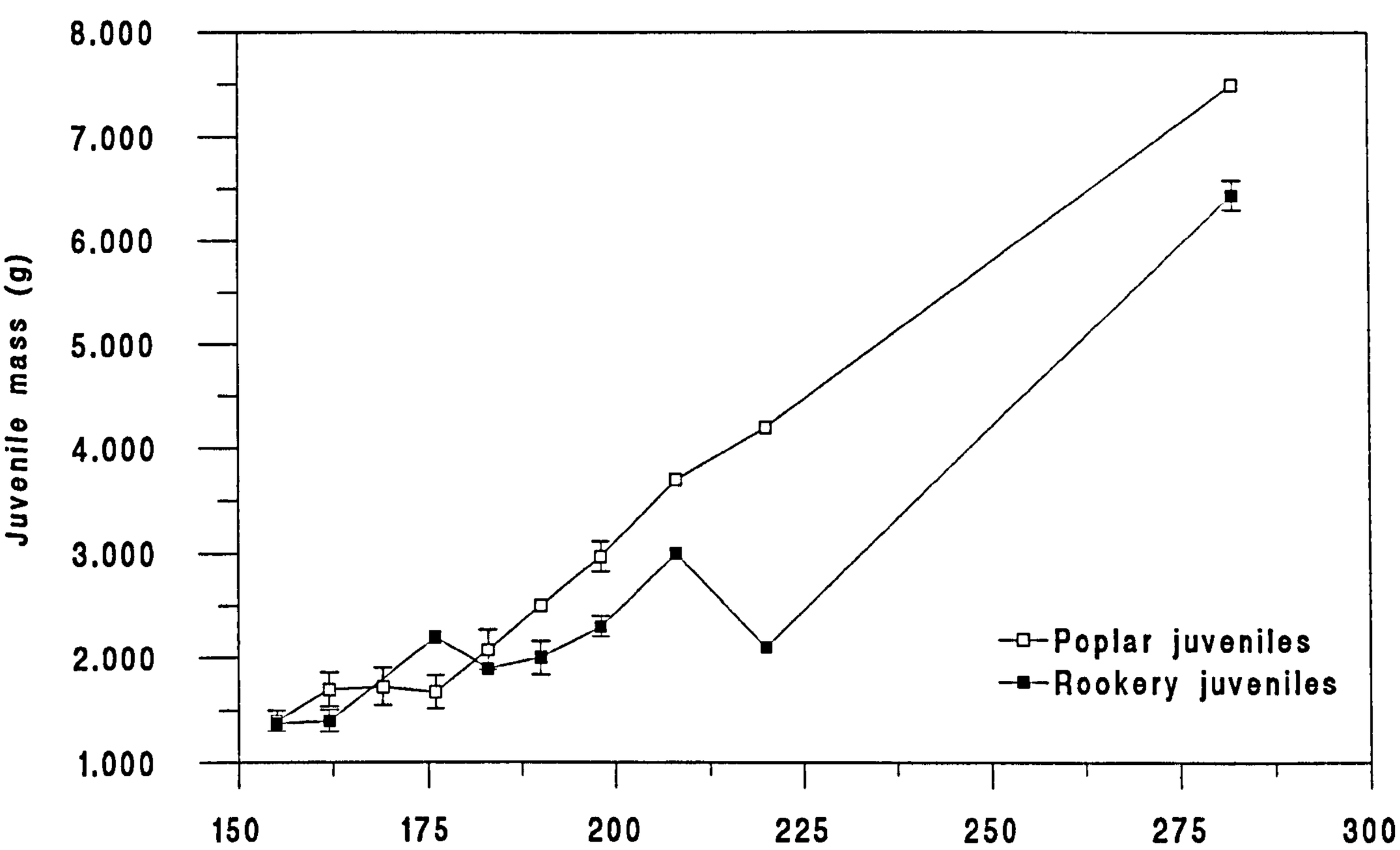

Figure 8.6: Comparative growth rates for juveniles (with standard errors) placed in enclosures constructed in the Rookery and the Poplars, Osbaston 1994.

TABLE 8.9: Variation in the mass of metamorphs during emergence from the lake, 1992-93. One way analysis of variance for data representing the early, mid and late emergence for LW in 1993 showed significant variation in mass (ANOVA, F_2=208.28, p<0.1). For 1992 there was a significant difference between the masses recorded during the early and late emergence (ANOVA, F_2= 6.68, p<0.1)

	1992			1993		
	Early	Mid	Late	Early	Mid	Late
Lake West	0.114	*	0.134	0.210	0.239	0.170
Lake East	0.151	0.191	0.155	No pattern observed		

TABLE 8.10: Length (mm) for metamorphs emerging from the Lake at Osbaston, summer 1993. There was no significant difference between the body lengths of metamorphs from each of the banks of the Lake (ANOVA F_3 = 1.18, p =0.317).

Side	n	Mean (± SE)	Median
Lake North	45	11.45 ± 0.17	11.00
Lake South	50	11.40 ± 0.15	11.25
Lake East	26	11.73 ± 0.28	12.00
Lake West	200	11.58 ± 0.10	11.50

compared with 13.8 ± 1.2mm for metamorphs caught at in the arable field to the west of the breeding site and 14.4 ± 1.8mm at the Spinney. Body length indicated a growth rate of 0.18mm/day, giving a very rough estimated size of 19-24mm at first over-wintering. It is estimated that a metamorph might increase its length by 70% during the six months from emergence to first wintering.

8.2.2.2 Juvenile growth

Juvenile growth estimated by study of the length of individuals that were trapped during the breeding season or caught during searches then aged using skeletochronology. Analysis showed a decline in the growth rate to 35-40% between 12 and 36 months from that during the first six months after emergence.

During the first 30 days individuals grew at a similar rate in each of the habitats, Figure 8.6. After day 210, however, the growth in the Poplars was more pronounced and by the final sampling day the Poplar juveniles appeared larger than those in the Rookery. Comparative growth rates were 0.039g per day in the Rookery and 0.048g per day in the Poplars. This amounted to a 14% difference in the mass of the juveniles at the end of the experiment, Table 8.11.

Juvenile growth in contrasting habitats was studied using enclosures constructed in the Rookery and the Poplars. The enclosures were searched for animals on a weekly basis between days 155 to 282. The number of animals found on each sampling day inside the enclosures constructed in the Rookery and Poplars varied during the experiment. On some sampling days only single animals were found, and thus it was impossible to calculate standard errors.

During hot weather the earth around the enclosures cracked, providing escape routes and small mammals could burrow under the fence and chew through the 'Netlon'. Routine maintenance identified any damage to the fence, however, the enclosures were unlikely to be 100% efficiency. Predation of the metamorphs was also possible; evidence suggested that thrushes used the slates in the enclosures for anvils and shrews could also chew through the netlon and prey on any juveniles. It seems likely that the decline in catch was a combination of mortality and escape.

TABLE 8.11: Increases in the mass of juveniles from enclosures constructed in the Poplar plantation and Rookery, June-October 1994. 1: Sample day, days since 1st January 1994. * only one individual found, therefore no error bar

Sample Day[1]	Poplars	Rookery
155	1.400 ± 0.100	1.375 ± 0.105
162	1.700 ± 0.163	1.400 *
169	1.725 ± 0.180	None found
176	1.675 ± 0.160	2.200 *
183	2.075 ± 0.190	1.900 *
190	2.500 *	2.000 ± 0.160
193	2.967 ± 0.140	2.300 *
208	3.700 *	3.000 *
220	4.200 *	2.100 ± 0.140
282	7.500 *	6.450 ± 0.350

8.2.3 Adult cohort

8.2.3.1 Adult growth and survival

Adult growth was calculated by analysis of recaptured animals. Although animals were not given individual tags, the combination of toe-clip and panjet mark permitted animals to be identified in terms of the year they were first caught, the location of that first capture and if the animal had been re-captured subsequently. Growth was calculated by comparing the difference in length between the set of untagged animals, assumed to be new adults that year, and the set of animals re-captured in the same habitat one year later. The difference in length between the re-captures and the new animals was expressed as a percentage increase in length. Thus each groups of tagged recaptures could be attributed to each habitat[3], and growth was estimated for the Rookery HSE (n = 30), Poplar HSE (n = 63) and for the Arable habitats (n = 12).

Annual growth rate between 1992-93 and 1993-94 was higher in the Poplar HSE (3.3%,) than the Rookery HSE (3.0%). Growth rate in the Poplars was, however, more variable than that estimated for the Rookery HSE, Table 8.12. The annual adult growth rate in the Poplar HSE fell from 1992-93 figure of 5.2% to 1.4% for 1992-94. In the Rookery HSE the growth rate increased from 2.5% for 1992-93 to 3.4% for 1993-94. For the Arable habitats, growth rate was estimated to be 5.7% for the 1992-1993 period, but a negative rate was observed in 1993-1994. Growth could not be calculated for the rough pasture due to the lack of availability of data from previous years for inclusion in the current study.

Survival was defined as the number of individuals tagged and recaptured in subsequent years, compared with the number of animals marked during the previous year. This definition assumes that there is an equal chance of capture at each of the habitats and that the chance of capture is consistent from year to year. As discussed in Chapter 6, trapping effort was higher in the woodland habitats (Poplar HSE, Rookery HSE in particular) than the arable habitats (AW and AN) and this might influence the results. However, survival in the woodland habitats was over twice that

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[3] Where n represents the number of recaptures used to compare DLU with the previous year

observed in the arable habitats, Table 8.13. Survival in the rough pasture was higher than that in the arable, but lower than that estimated for the woodland. It is, however, likely that the figure representing the pasture for 1992-93 survival was an underestimate, since trapping was not continued in 1993. There was a significant positive correlation between male survival and adult density within each habitat ($r = 0.378$, $p < 0.05$).

Small recapture figures[4] for females meant survival could not be calculated for individual habitats, however an inter-year survival of 25% was estimated for the combined recapture data over all habitats. This figure is lower than the highest shown in the male population (35%). It is possible that the extra stress in breeding and egg production and loss of females by drowning during breeding could increase the mortality of females.

8.2.3.2 Population size

Male population was calculated using the a MRR method. The female population was calculated on the basis of the proportion of females in the nett catch from the trapping exercises. The male population declined by 50% over the period 1992-94. The decline was greatest between 1992 and 1993, when the male population fell by one-third. The male population fell by a further 25% between 1993 and 1994. In contrast, the female population remained fairly consistent over the period. Overall, the estimated adult spring population at Osbaston Hall declined by over 40% between 1992 and 1994, Table 8.14.

8.2.3.3 Fecundity

The mean fecundity of a sample of 30 females derived from Osbaston Hall over the period 1992-1994 was 1941 eggs/female (SD = 672), with a range of 870 to 3460. A smaller sample of 10 individuals collected from Little Wittenham in 1995, showed a slightly smaller mean of 1654 eggs/female (SD = 520), with a range of 804 to 2267. The fecundity from the two sites was not significantly different (Mann-Whitney = 0.303,

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[4] Based on that there are fewer females in the adult population and that survival is slightly lower for females.

TABLE 8.12: Estimated adult annual growth 1992-93, 1993-94 for males caught and recaptured in the rookery (n = 30) and poplars enclosure (n = 63) and at the arable west drift fence (n = 12). 1: New animals (untagged in 1992 or 1993). 2: Mean length of recaptures first marked in 1992 or 1993 and recaptured in subsequent years.

	1992-1993			1993-1994		
	New[1]	Re-caps[2]	Growth	New[1]	Re-caps[2]	Growth
PPI	53.5 ± 0.4	56.3 ± 1.7	5.2%	51.8 ± 1.7	52.5 ± 1.4	1.4
RKI	54.5 ± 0.3	55.8 ± 1.5	2.5%	53.0 ± 0.8	54.8 ± 1.4	3.4
Arable	52.2 ± 0.6	55.3 ± 0.8	5.7%	55.8 ± 4.2	54.1 ± 1.7	*

TABLE 8.13: Adult male survival, Osbaston Hall 1991-94. 1: Calculated as a % of adult male toads recaptured in any habitat and tagged in the specific habitat in the previous year. 2: Calculation may be an underestimate since rough pasture fence lines were not operative in 1993 and thus trapping effort was reduced, no adults were tagged specifically for pasture in 1993, thus no further survival estimates may be calculated

Habitat	Inter-year adult survival (%)[1]		
	1991-92	1992-93	1993-94
Arable	16	10	17
Rookery	35	27	35
Poplars	28	43	30
Pasture	18	12[2]	N/A

TABLE 8.14: Adult population size at Osbaston Hall between 1990-1993. 1: Male estimate gained from MRR exercise (see Chapter 6). 2: Percentage of catch female. 3: Data from Halley *et al.* (1996). 4. Total population calculated using estimated male population size multiplied by the proportion of total female catch

	1990[3]	1992	1993	1994
Male estimate[1]	2500	3000	2000	1500
Female estimate[2]	900	600	400	500
% Female	36	20	21	29
Sex Ratio	Not known	4.4:1	3.8:1	2.9:1
Total[4]	3400	3600	2400	2000

Figure 8.8: Age (as determined by skeletochronology) toads caught during the breeding season, over 1991-1994.

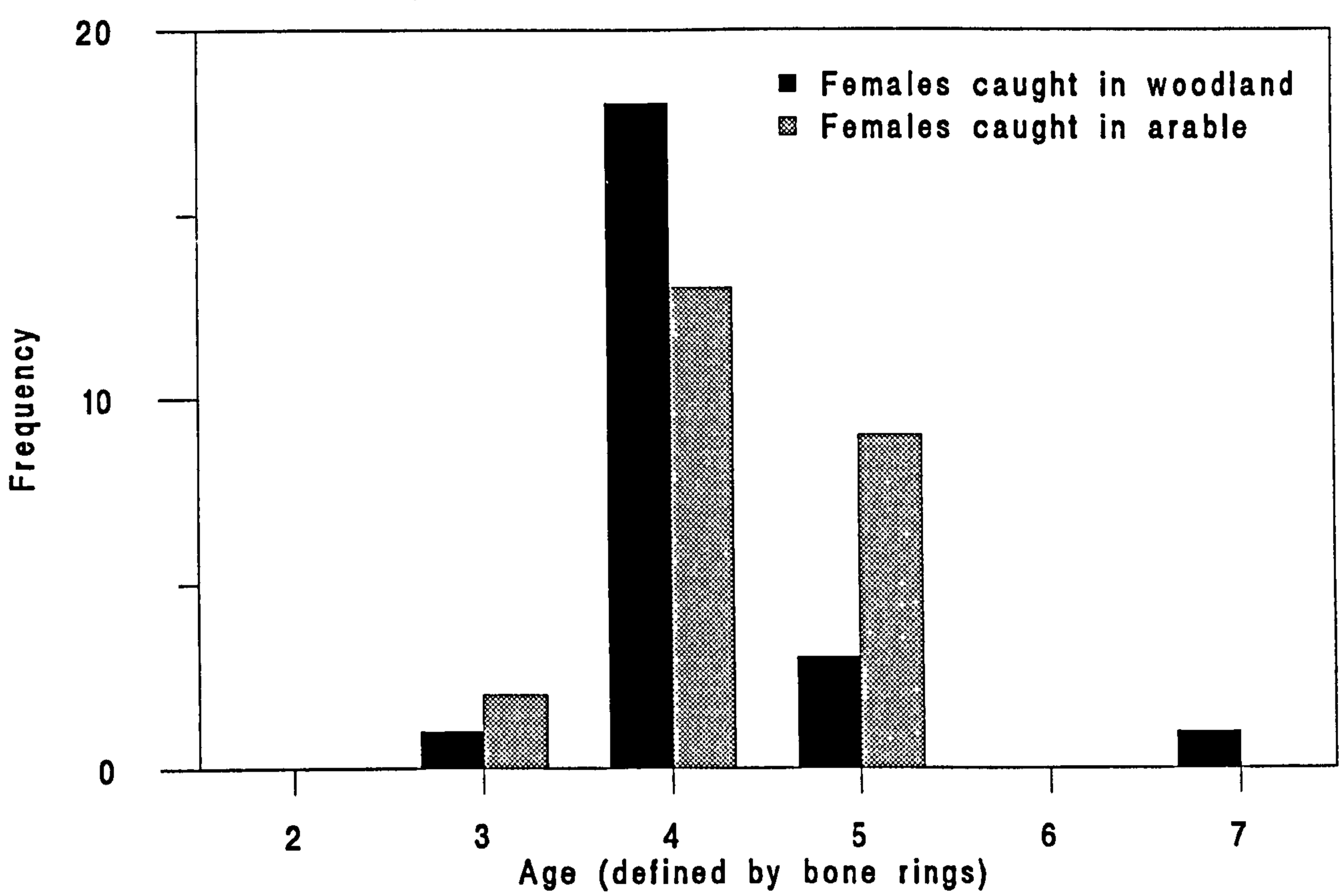

Figure 8.13: Age (as determined by skeletochronology) of breeding females over-wintering in woodland and arable sites.

$p > 0.05$).

For both sites the fecundity was positively correlated ($p < 0.01$) with body length (Osbaston $r = 0.634$, Little Wittenham $r = 0.780$). At Little Wittenham, fecundity showed a negative correlation with body condition ($r = -0.539$, $p < 0.05$), with females showing a higher condition index surprisingly holding fewer eggs[5]. This is a particularly unexpected result given that previous research by Kuhn (1994) showed that both fecundity and total egg volume were positively correlated with female condition. A possible explanation for the unusual Little Wittenham result might be a variation in egg size, given that Kuhn (1994) also showed a negative relationship between egg number and size. No measurement of egg size was completed for the current study. The r^2 statistic (0.289), however, shows over 70% of the variation is accounted for variables than body condition. Lack of raw data on female lengths, mass and corresponding fecundity for individuals prevented similar analysis at Osbaston.

The body length/fecundity relationship has been described by Gittins *et al.* (1984) as a *triangular zone* rather than the simple linear relationship defined by Davis and Halliday (1977). Figure 8.7 is a composite of the results from Osbaston and Little Wittenham and from previous studies where fecundity has been calculated (Halliday and Davis 1977, Gittins *et al.* 1994, Banks and Beebee 1986). There is clearly a maximum limit to fecundity (maximum potential fecundity MPF) of a female of a given size and collective data suggest there is also a minimum viable fecundity (MVF) of about 600 eggs.

8.2.3.4 Age structure and dynamics

Toe sections from 150 adult individuals (males and females), collected from Osbaston during the breeding seasons 1991-1994, were selected for age determination. Of these, 88% produced sections where the number of rings could be counted and the age estimated, the remaining sections were folded or failed to absorb the stain clearly enough to show the stain. The oldest individual was a single female estimated to be eight years old, while several males were estimated to be five years old, Figure 8.8.

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[5] The condition index used the mass of females prior to spawning.

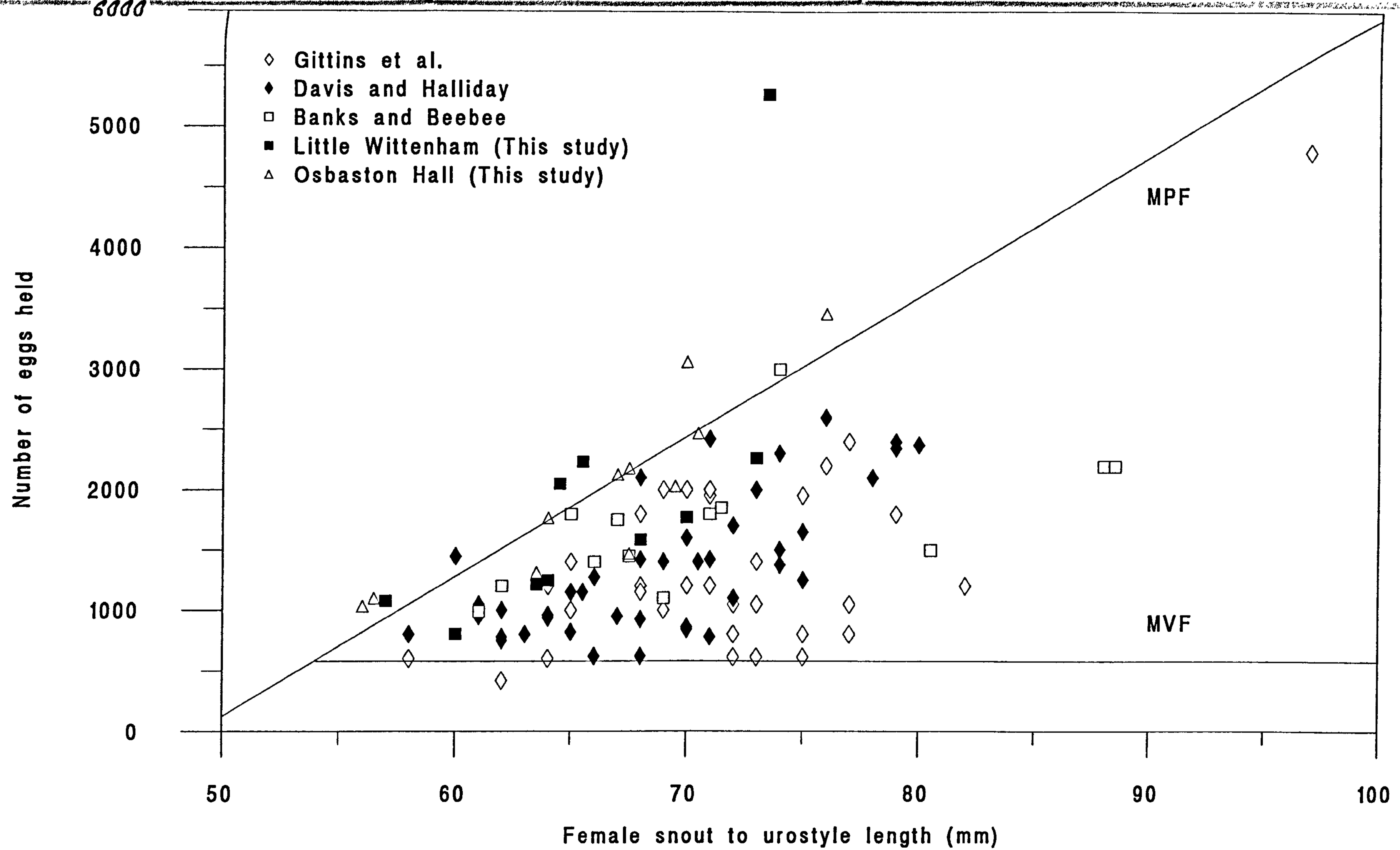

Figure 8.7: Relationship between female body length and number of eggs laid from Osbaston Hall Estate and Little Wittenham. Three addtional studies are provided for reference. MPF: Maximum potential fecundity, MVF: Minimun viable fecundity

Age was significantly correlated with the body length of toads (product moment correlation, r = 0.759, p <0.01), with the r^2 (0.576) indicating that 60% of the variation in length was described in the regression with age (for a combined sample of females, males and juveniles), Figure 8.9. However, this relationship was largely accounted for by the inclusion of those toads aged two or under. Removal of the juveniles weakened the relationship, in particular the coefficient of determination, although it still remained significant (product moment correlation, r = 0.425, p <0.05, r^2 = 0.181), Figure 8.10. The age/length relationship was weaker for adult females (product moment correlation, r = 0.077, p >0.05), Figure 8.11, than for adult males (product moment correlation, r = 0.309, p >0.05), Figure 8.12.

The ages of 50 females between 50 and 70mm caught at the Arable North (AN) drift fence and in the Rookery HSE (RKI) were compared, Figure 8.13. It is assumed that these animals would be first time breeders; judged to be reasonable given the available information on inter-year survival. The RKI and AN catches were selected since there was little or no migration between these habitats and only females were selected since it was assumed that they would offer a better comparison. Results from Chapter 6 appear to suggest that the need for resources for both growth and egg production exposes any variation in habitat quality more clearly for females than for males.

The mean age of the females caught at RKI was 4.0 years compared with the mean age of 4.38 for the females caught at AN. The majority of the sample caught in both habitats were four years of age. However, 36% of the females caught from AN were aged five years compared to only 13% of those derived from the RKI. Given the assumption that these females were caught during their first breeding migration as sexually mature adults, a higher percentage of females using the arable habitats took five years of age to reach sexually maturity than in woodland habitats. This observation was backed by the slightly higher mean age for the whole arable sample. Two females aged seven were caught at RKI, however there were no females aged over five years of age caught at AN, suggesting that survival beyond a single breeding attempt was lower in the arable habitat than for the Rookery.

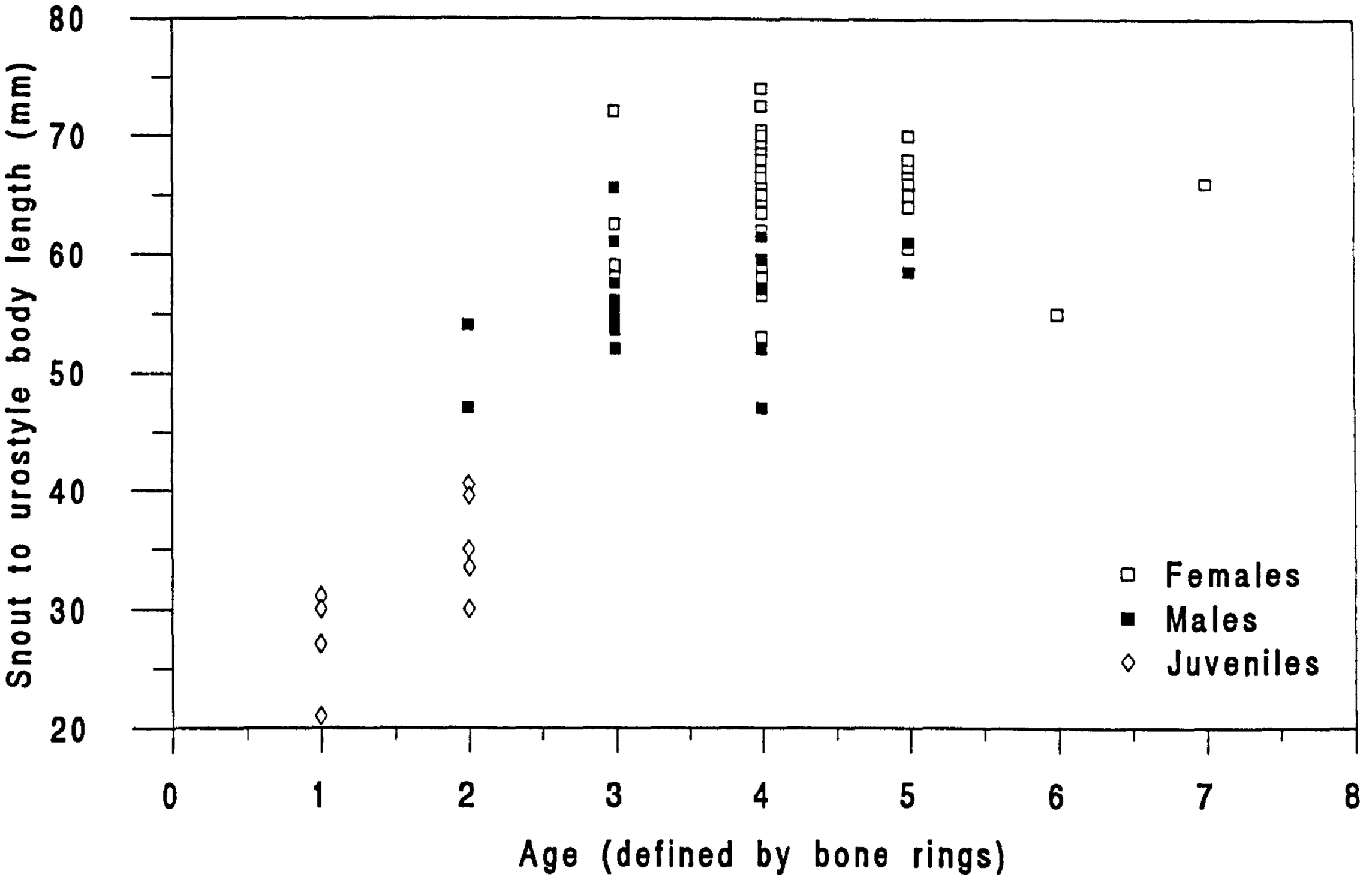

Figure 8.9: Relationship between body length (mm) and age (as determined by skeletochronology) for indiviudals caught at Osbaston Hall, 1990-1994.

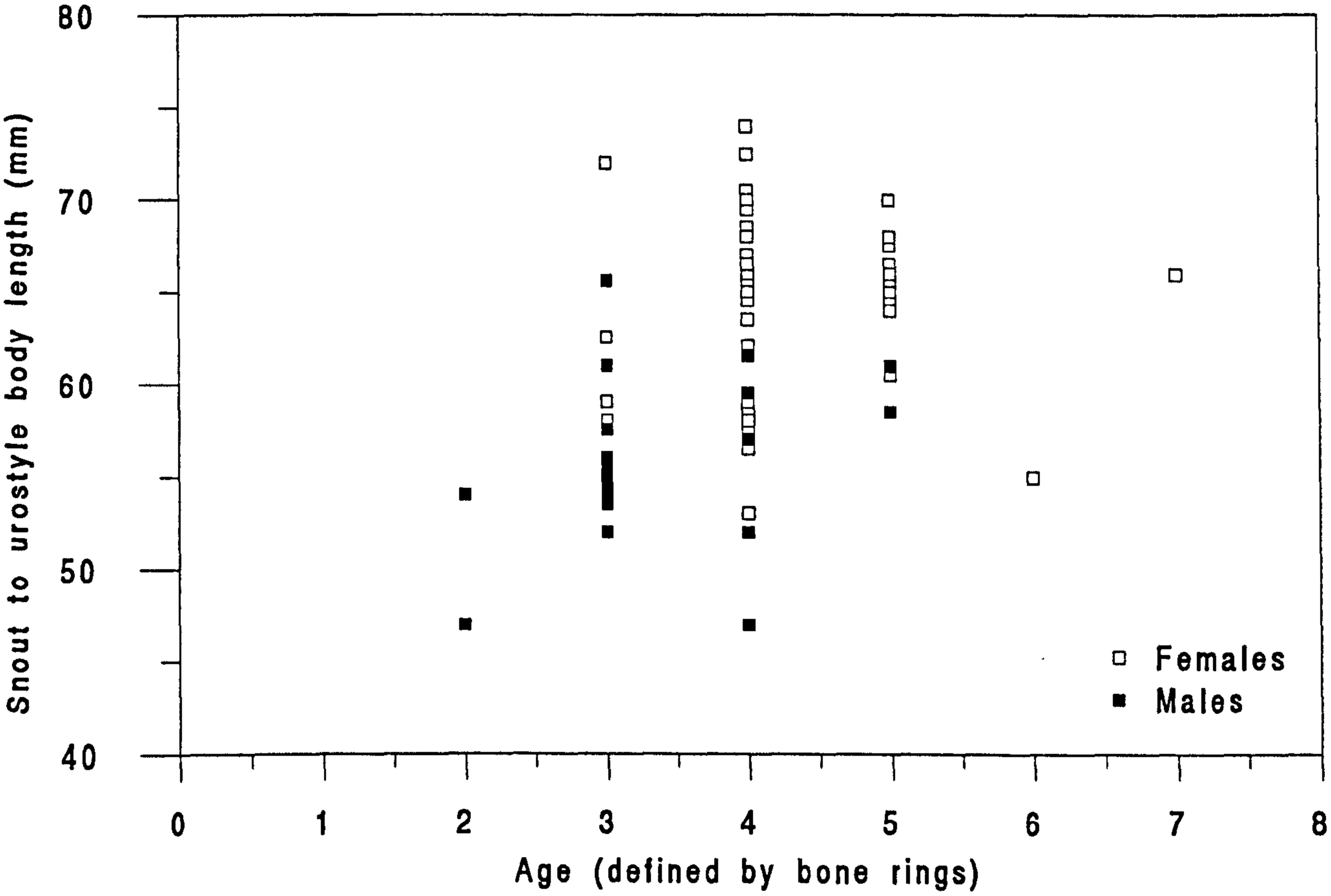

Figure 8.10: Relationship between body length (mm) and age (as determined by skeletochronology) for indiviudals caught at Osbaston Hall, 1990-1994.

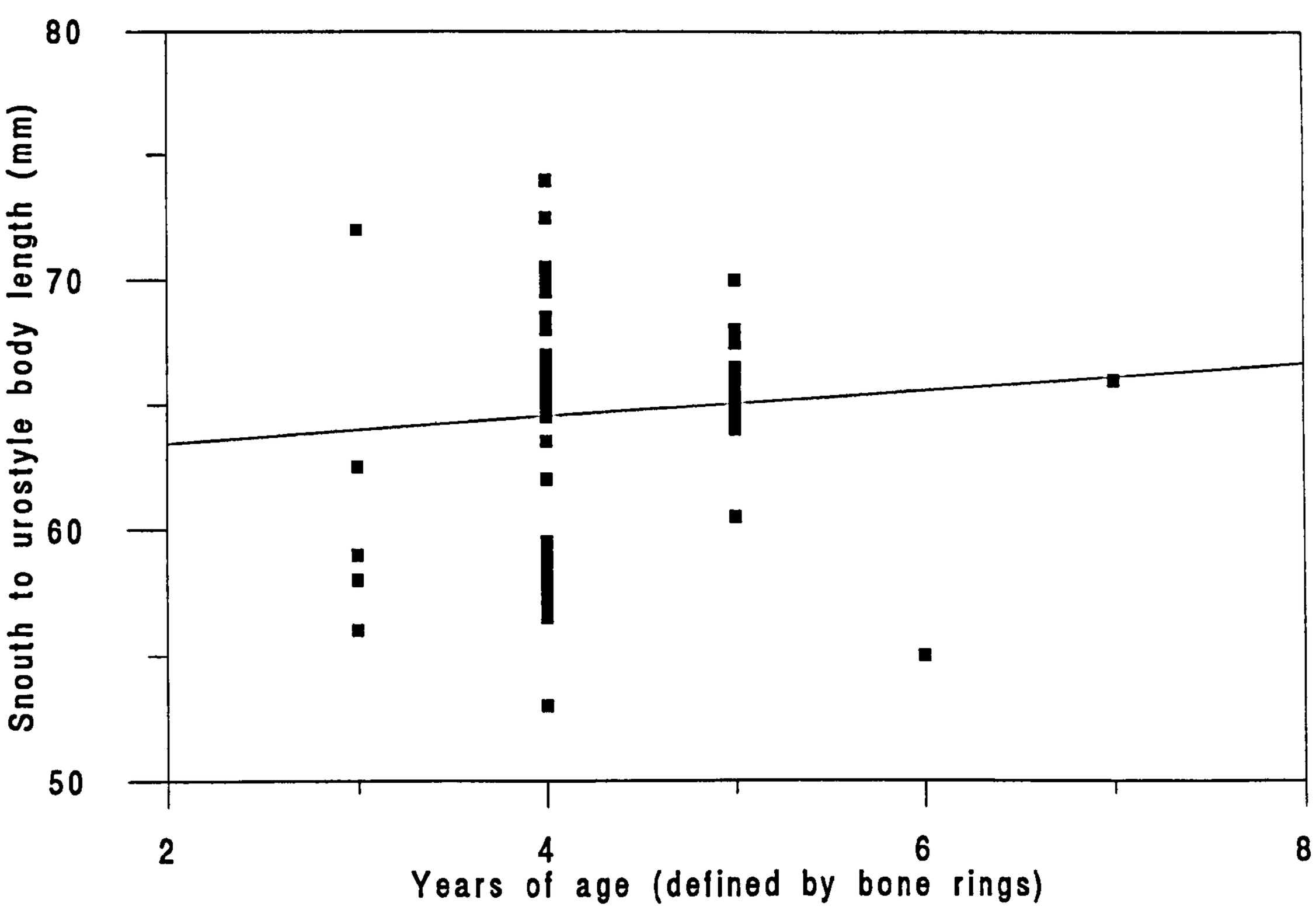

Figure 8.11: Relationship between body length (mm) and age (as determined by skeletochronology) for females caught at Osbaston Hall, 1990-1994.

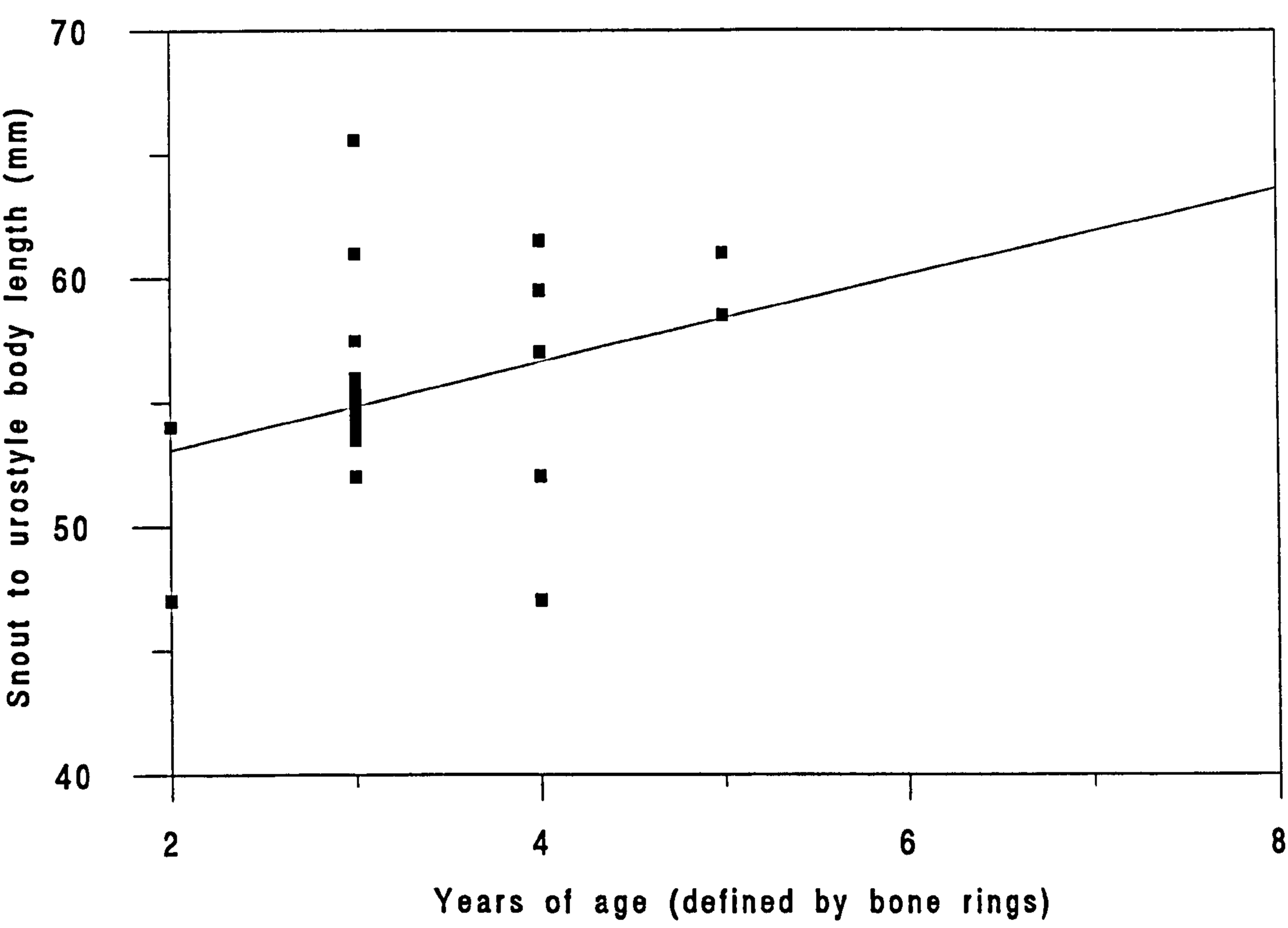

Figure 8.12: Relationship between body length (mm) and age (as determined by skeletochronology) for males caught at Osbaston Hall, 1990-1994.

8.3 Discussion

8.3.1 Size at metamorphosis

Results from 1991 and 1992 are less than satisfactory given errors missing the first part of the emergence and preserving the samples. The most complete set of samples was collected in 1993, and this has formed the most valuable for further analysis.

In 1993, there was a characteristic increase in the mean mass at emergence for each day during the first half of the emergence from the pond at Osbaston Hall, followed by a decline once the majority of metamorphs had left the water. The rise could be explained by a reduction in competitive stress, producing greater food resource opportunities. Travis (1984) showed a positive correlation between size at metamorphosis and length of the larval period for *Hyla gratiosa*. This hypothesis, however, fails to suitably explain the observed decline in mass during the second half of the emergence period that was clearly apparent for the Lake in 1992 and 1993. Moreover the rise in mass occurred over only five days, and it seems unlikely that changes over such a short period of time could have a significant effect on emergence mass.

Size at metamorphosis is considered to be a reflection of the resources available during larval development for anurans (Wilbur and Collins 1973, Wilbur 1976, Wilbur 1977, Collins 1979, Dash and Hota 1980, Wilbur 1980, Werner 1986). Competitive stress may result in tadpoles that metamorphose at a smaller size, or an increase in the length of the larval period (Wilbur 1976). Competition for resources can manifest itself through mass at metamorphosis and/or the length of larval period; intra-specific competition was believed to increase, and resource availability decline for two species of salamander, *Ambystoma maculatum* and *Ambystoma laterale,* and the wood frog *Rana sylvatica* (Wilbur 1976) as larval density rises. A decrease in mass at metamorphosis during the emergence period would be expected if there was a size advantage operating during the larval period; with the larger larvae out competing the smaller individuals for high quality food resources, reaching the size required for metamorphosis and emerging first (Steinwascher 1979). Although there appears to

be a downward trend in the mass of metamorphs emerging from the LW in 1993 in the current study, those metamorphs emerging from the mid-part of the season were significantly larger than those during either the early or late part of the season. Size advantage due to variation in egg size has been shown to be continued throughout the larval period, for one species of salamander (Pechmann *et al.* 1988). However, common toad eggs show little variation in size (Oldham pers. comm.).

The common toad has a short spawning period (Chapter 6) and development within the tadpole population is relatively uniform with metamorphosis and emergence occurring over a short period. This is reflected in the current study where over 40% of the total metamorph output left the pond during the peak emergence which lasted only 1-2 days for each year (Chapter 6, Figure 6.13). Metamorphs were observed to aggregate during the final days prior to emergence. The positive effect of the pre-metamorphic aggregations at Osbaston would have been enhanced by the larger group size immediately prior to peak emergence; increased interaction in larvae of *Bufo americanus* increased the mass at metamorphosis due to access to faeces and social facilitation in feeding, allowing the break-up of larger food sources by a larger group (Breden and Kelly 1982). Those metamorphs that had reached a suitable size for metamorphosis before or after the main group would not benefit from this final association and thus metamorphose at a smaller size.

An alternative hypothesis to explain the variation relates to the trapping technique used at Osbaston Hall. The metamorph traps were open to capture animals from the land side, in addition to those moving out of the water. There is some possibility that animals might have been caught following a period already on land. This hypothesis is backed by the observation that the percentage of the metamorphs emerging with complete tails fell during emergence. It is observed that during the last few days of metamorphosis the mass of the individual falls, as tail absorption takes place. Newly emerged animals do not forage, but gain their energy requirements through absorption of the tail. Indeed, although not significant, mass declined over the five stage of tail absorption, Tables 8.3 and 8.4. The rise in mass could not be entirely attributed to an increase in the number of animals at a later stage of development, as there was no significant difference between the means of metamorphs at the six development

stages (in 1993). Whilst the initial rise in the mass at emergence could be explained by the benefit of an increased larval period or reduction in competitive stress, the subsequent fall might reflect those individuals that had left the pond some few days earlier.

8.3.2 Productivity of the Osbaston aquatic habitat

The highest mass at emergence at Osbaston Hall was 0.210 ± 0.001g in 1993, whilst the lowest mass was 0.115 ± 0.001g in 1992. The highest mass was recorded when emergence was greatest. Ryszkowski and Truszkowski (1975) found the biomass of newly emerged *Bufo bufo* metamorphosed metamorphs to be 2.1g from small ponds located in arable fields. Metamorphs emerging from a site at Coleorton, Leicestershire had a mean mass of 0.381 ± 0.009 during 1993 (Latham, unpublished). In previous years the pond had produced slightly smaller metamorphs, with a mean of 0.25g (Oldham pers. comm.). Metamorphs from three sites collected from Thetford Forest in 1994 were 0.233 ± 0.050, 0.200 ± 0.008 and 0.181 ± 0.005 (Latham, Gibbons and Oldham, unpublished data). McEvoy (1995) provides the mass of metamorphs caught after emergence for 17 sites in north-west Leicestershire, all within 20 miles of Osbaston Hall. In her study masses ranged from 0.095 to 0.347 with a mean of 0.225g. The 1993 mass at Osbaston would rank 11 in McEvoy's study, whilst the 1992 mass would rank 16. On the basis of these data, it appears that Osbaston is a relatively poor aquatic habitat.

The mean mass at emergence of metamorphs was variable from year to year during 1991-1994 at Osbaston Hall. Despite this variation there was some consistency in the size of metamorphs emerging from each part of the Lake within each year of the current study. There was some variation in the physical condition of adult toads returning from the different habitats at Osbaston, but this variation was not attributable to the direction (ie north, south, east or west) of their breeding migration. No clear variation in adult size was determined between the various habitats (Chapter 6). The consistency in the size of the metamorphs on emergency from the Lake in contrast to the variation in condition of adults from certain habitats suggest that the regulating force for the toad population at Osbaston was stronger during the juvenile terrestrial stage than the aquatic phase. Final adult size has been related to size at

metamorphosis for the chorus frog, *Pseudacris triseriata* (Smith 1987), and for the common frog (Cummins 1989) with small metamorphs becoming small adults. Smith (1987) showed that the prime force in shaping the size of adults of the chorus frog was the size at metamorphosis, resource availability within the aquatic stage having a lasting influence on the species into the terrestrial stage. For the Osbaston population, it is the quality of the habitat used by the toad during its juvenile stage that shapes condition rather than perhaps the experience during the larval stage.

It is proposed that food limitation is the likely force shaping metamorph success at Osbaston. Low or decreasing food per capita caused tadpoles of the desert spadefoot (*Scaphiopus couchii*) to metamorphose at a uniformly small size, but the emergence was not synchronous and individuals varied in the time required to attain the emergence size (Newman 1994). Similarly, *Rana tigrina*, tadpoles under high densities decreased the threshold size for metamorphosis in comparison to lower density populations (Dash and Hota 1980). The variable output and consistently low mass at emergence at Osbaston Lake suggests that the water body is a poor habitat for larval amphibians. The larval stage at Osbaston lasted between 76-110 days[6] (Chapter 6), which is comparable to the 65-106 days in the south-east and 85 days in mid-Wales (both figures quoted by Slater 1992). The comparable length of larval period appears to reflect the balance to emergence at a slightly smaller size rather than to increase the length of the larval stage. Given an already limited food resource it may be more beneficial to emergence from the pond and commence feeding on land rather than attempt to achieve a larger size at metamorphosis by remaining in the aquatic environment.

8.3.3 Post-metamorphosis dispersion

Oldham and Swan (1991) compare the dispersion of juveniles into the surrounding terrestrial habitat following emergence from the breeding site to an ever-increasing wave. Metamorphs are believed to continue to move away from the breeding pond

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[6] Based on the difference between the date of first spawning and the first emergence and the date of the last spawning and final emergence.

until colder weather reduces their activity. In their second year animals are unlikely to have grown sufficiently to have achieved a viable size for breeding and therefore do not migrate towards the pond. It is assumed, therefore, that the juveniles remain at the distance achieved after exodus from the pond in their second summer. This location will form their summer home-range, which is believed to be maintained throughout the life-time of the individual.

The habitat is selected following the random emergence from the natal pond, and ease of movement, rather than any process governed by the suitability of habitat. After the second over-wintering period some of the males may be close to a viable size for breeding and may migrate to the pond. The smaller animals will not migrate and it is suggested that these will remain in the ranges established in previous years. Once the animals have successfully bred, animals return to their established ranges.

This hypothesis suggests a non-specific form of habitat selection. Davis and Krebs (1991) provide the theory of optimality to describe animal habitat selection, based on the ability of any habitat to provide the necessary requirements for survival for a given species. Under optimality an animal will select the habitat that best matches its requirements. The selection patterns proposed for the common toad can be likened to the behaviour of spell-bound Titania, the Fairy Queen in Shakespear's *A Midsummer Night's Dream*, who fell in love with the first thing she saw on waking, despite its unsuitability. Similarly, it is proposed that the toad remains faithful to the first habitat it experiences, despite the potential that the habitat selected is less suitable than habitats within a similar dispersion distance from the pond.

8.3.4 Impact of habitat on juvenile growth and survival

Comparison between the growth of juveniles, indicated a slower growth in the Rookery than the Poplars given an equal density (0.6 juveniles/m^2). At the end of experiment the Rookery juveniles were 14% lower in body mass than those from the Poplars. Survival may be reduced in smaller, slower growing juveniles, since smaller animals are unable to exploit the larger prey items that may offer a higher food benefit. Rookery adult males were in significant poorer condition than other males. Cohen and Alford (1994) showed that the growth rate of cane toad metamorphs (*Bufo marinus*)

was slower at high densities (16.7 metamorphs/m^2) than metamorphs at lower densities (3.3 metamorphs/m^2). This evidence may suggest that the differential success in supporting the juvenile cohort of a population in the various terrestrial habitats, reflected in the lower growth rate of the juveniles released in the Rookery may have some control in determining the size of individuals as adults.

It is hypothesised that in a fragmented landscape, like Osbaston, where habitats of a variety of qualities are available to the toad, it is more likely that the carrying capacity of each habitat will be a stronger force in shaping initial growth and survival in the metamorph-juvenile cohort than the initial density. This theory is based on the dispersion of the metamorphs from the pond after metamorphosis that occurs as an increasing wave out into the surrounding landscape (Oldham and Swan 1991). If emergence from the pond was consistent throughout its perimeter then the initial input of metamorphs into the surrounding habitats could be assumed as equal. Results in the current study indicated that dispersion by metamorphs from the breeding site at Osbaston was not influenced by the nature of the habitat, bar the actual speed of travel. Metamorphs were caught in traps located in the arable field to the west of the breeding pond during dry periods and continued to use the habitat even after harvesting and ploughing. After dispersion into the surrounding habitats, some densities may be above the habitat's carrying capacity. Higher mortality will occur where habitats have an input of recruits above their carrying capacities.

Changes in the density of the juvenile population will be dependent on the suitability of habitat for this life-stage. Thus, I believe in the current study it is the terrestrial habitat quality that governs growth and survival in the metamorph-juvenile cohort rather than the initial density. This hypothesis does, however, assume that inferior habitats are 'over-crowded' at the start of the process.

8.3.5 Adult survival

Survival from year to year was estimated to be less than 40% for the adult male population. Gittins (1983b) provides a figure for annual male survival of 52%, whilst Cooke and Oldham (1995) estimated a value of 36% for a relocated population. Survival was highest in the woodland habitats and lowest in the arable habitats and

this pattern was consistent throughout 1991-1992, 1992-3, 1993-1994. For females survival was lower (given the increased pressure of reproduction) and estimated to be only 25%. This conclusion is consistent with the assumption that woodland habitats are of higher value than arable habitats for the toad. The year to year survival of less than 40% shows that in each year, given a consistent input of juveniles, the majority of animals are first-time breeders and that the turnover of the population is high.

Kuhn (1994) provides a higher rate of survival in population in southern Bavaria, with a maximum winter mortality of 40%. It is however, suggesting that it is a minority of females that manages to reproduce repeatedly, but females may breed in intermittent years, as also stated by Gittins et al. (1980). The short period given for the current study did not permit the opportunity to develop this concept.

8.3.6 Fecundity

Cited literature (Gittins *et al* 1980, Banks and Beebee 1986, Davis and Halliday 1977) confirms a minimum number of eggs held by breeding females and the current study suggests that females in poor condition may not breed. Gittins *et al.* (1980) suggest that females may intentionally miss a breeding season to concentrate on body growth rather than egg production, since this may improve the opportunity for survival. Berven (1990) showed a negative correlation between fecundity and population density. The negative correlation between fecundity and body condition shown for the toads at Little Wittenham suggests that there may be resource limitation even in prime habitat.

The common toad is a typical 'r' strategist, producing a high number of potential offspring each year with the absence of parental care. It seems unlikely that females should forgo the opportunity to breed each year to concentrate on body growth. The average life expectancy of a female toad from emergence is 6 (Gittins, Steeds and Williams 1983, Gittins, Kennedy and Williams 1985), providing a maximum opportunity to breed only three times during its life time. It seems more likely that females will breed at each annual opportunity, despite holding fewer eggs than their full potential. Although this contradicts the assumption in Chapter 6 that females in poor condition do not breed.

8.3.7 Age distribution and age at maturity

Variation in body-length of the adult may be influenced by variation in the age at maturity. The effect of delaying breeding is shown when comparing the age of the females caught in the arable fields and their counterparts in the Rookery HSE, both sets of animals were assumed to be first time breeders. Whilst the mean age for each habitat was similar, a higher proportion of the toads from the arable fields were five or more. The females caught in the arable appeared larger than those from the Rookery HSE (1993: length arable north 66mm compared to 62mm for the Rookery HSE, Chapter 6), although the length differences were not statistically significant. Kuhn (1994) provides a similar conclusion indicating that reproductive maturity was linked to length rather than age and that where females that grew more slowly could be larger when reproducing for the first time than females that grew faster.

The difference may be explained by comparing development strategies; in year four some of the arable females may not have reached the minimum size required for breeding, in contrast to the majority of Rookery HSE females. In year five those arable females that failed to breed in year four migrate for the first time, by now they are larger than would be expected as first time breeders due to an additional year's growth as a juvenile.

8.3.8 Dispersion, population fluctuation and regulation

The Osbaston population has remained large[7], but has not reached a level where it could be described as exceptional. No significant changes occurred in land management of the estate during the study period, bar rotation in the arable crops, however, there has been a noticeable decline in the adult breeding population over the study, particularly in the period 1993-94, Figure 8.14. The major cause of this decline appears to be poor metamorph output in 1991 manifested by a decline in the male population in 1994 and anticipated decline in the female population of 1995.

The year difference in the age at maturity between the two sexes will produce a lag

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[7] Any toad population over 500 adults is considered to be large under guidelines for the selection of biological SSSIs (Sites of Special Scientific Interest) and exceptional if the population is over 5000 (NCC 1989).

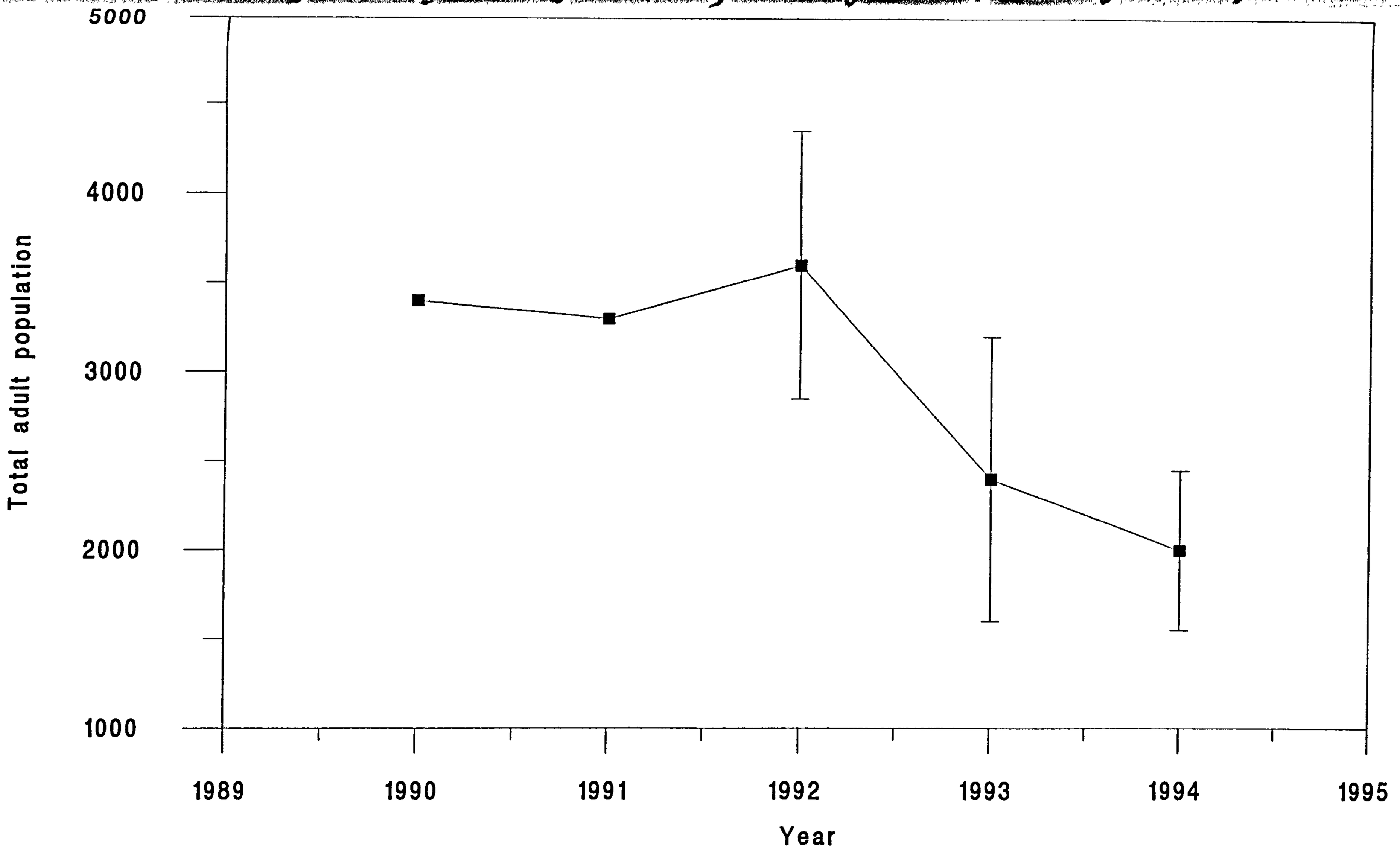

Figure 8.14: Changes in total adult population as determined by mark and recapture for males and proportion of gross catch for females, Osbaston Hall 1990-1994 (no standard errors available for 1990-1991)

between the impact of any breeding failure, i.e. the impact of the poor metamorph output in 1991 would not be seen in the new female cohort until 1995(6), whilst the impact would be shown in the previous year for the males. The sex-ratio has shown to fall in favour of females over the same period, from 4.4:1 in 1992 to 2.9:1 in 1994. Metamorph success was high in 1992 and 1993 indicating that a recovery in the adult population should occur over 1995-7 if this theory is correct. The breeding failure in 1994 suggests further decline, but would not manifest itself until 1997-8.

The adult survival during the study has shown most variation in the Poplars. The arable and Rookery HSE habitats have shown less variation. Given that the 'trespass' rate is highest for the Poplars, the calculation for survival for this HSE is likely to be less the efficient due to the mixed origin of animals caught there. The limited variation in survival between the years for the rookery and arable habitats suggests that the main factor causing the variation in the population size is probably unlikely to be identified during the adult stage.

The density of adults in the arable areas has remained consistent throughout the study (Chapter 6 and 7), however, the densities observed in the woodland habitats has varied from year to year. It is suggested, that the adult density in the arable habitats has been close to its carrying capacity throughout the study period. The woodland habitats showed higher densities than the arable habitats suggesting that these habitats had a higher carrying capacity than the arable fields. Fluctuation in the number of individuals entering the population as juveniles would manifest itself in changes in adult density in habitats below their carrying capacity, since a higher percentage of the juveniles would survive. In habitats where only a small number of individuals could be recruited, due to low carrying capacity, less fluctuation in the adult population would occur, as long as the carrying capacity was always exceeded.

The decline in catch discussed in Chapter 6 was highest in the most distal fences (SPI, AN and RKI). If we assume that the decline in population is primarily caused by a reduction in recruitment, excepting Oldham and Swan's (1991) hypothesis on the movement of metamorphs out from the pond following emergence. The catch data from the current study suggests dispersal may be widest during the juvenile phase,

since the decline in catch on the distal fences might be caused by a fall in new population recruits.

Females, on average, mature one year later than males and therefore have an additional year for migration away from the pond following exodus, this might explain the higher proportion of females caught at the fences over 250m away from the pond. Although it is advantages for males to locate close to the pond to ensure a breeding partner (Chapter 6).

For the common toad, where individuals are short lived with a high fecundity but low proportion of the potential off-spring incorporated into the population, regulation in terms of population size, has been attributed to the larval stage (Wilbur 1976). The adult population can saturate the larval habitat, however larval success is insufficient to saturate the adult habitat; the annual variation in the estimated density of adults in the woodland habitats suggests that its carrying capacity was never reached. This general hypothesis appears true where the available habitats are uniform in quality, however at Osbaston the varying adult densities in each of the habitats indicate a varying habitat quality, and thus the number of adults may be too low to saturate the larval habitat, but a sufficient number of juveniles are produced each year to saturate the adult habitat in poorer habitat.

The life-table for the common toad in Table 8.15 is based upon the data developed from the current study with additional information from Gittins (1982, 1983a 1983b) and Oldham (pers. comm.). Some caution should be applied to these data, given the accepted problems associated with sampling technique for the metamorphs. The technique could have exaggerated the total emergence and thus affected the estimates for survival into the juvenile stage. However on land, if these data are correct, the adult population comprises only 10% of the total autumn population. This figure is comparable to that cited by Oldham (1994) for a population within a similar landscape, although lower than the 15% cited by Oldham and Swan (1991).

Given these date it is estimated that over 90% of the mortality in the common toad population at Osbaston occurred among individuals at pre-metamorphosis. Survival

Table 8.15: Simplified cohort life-table for the common toad, additional sources of data provided in parentheses. 1: Egg number based on median fecundity multiplied by the estimated size of female population provided from MRR exercise. 2: Mortality back calculated from the number of metamorphs successfully emerging from the breeding site. 3: Extrapolation from the metamorph catch. 4: (Gittins 1983, Oldham pers. comm.). 5: Mean male mortality calculated from total catch. 6: Female mortality calculated from total catch. 7: Mortality stabilises and is considered to be independent of age after achieving adult status (Gittins 1983).

Age in years	Male			Female		
	Stage	Numbers	Mortality	Stage	Numbers	Mortality
0	Eggs[1]	1,125,000	90%[2]	Eggs[1]	1,125,000	90%[2]
0.3	Metams[3]	112,500	75%[3]	Metams[3]	112,500	75%[3]
1	Juvenile	28,125	70%[4]	Juvenile	28,125	70%[4]
2	Juvenile	8,431	70%	Juvenile	8,431	70%
3	Adult	2,531	65%[5]	Juvenile	2,531	75%[6]
4	Adult	886	65%[7]	Adult	633	75%
5	Adult	310	65%	Adult	158	75%
6	Adult	108	65%	Adult	40	75%
7	Adult	37		Adult	10	
Total (adult)		3,946	Male	Female	841	

is independent of age once adult status has been achieved (Gittins 1983b), although lower for the female. There is no reason to believe that there is a sex differential in survival prior to maturity.

The simplified life-table in Table 8.15 has been developed to determine age-specific mortality in Table 8.16 for males only, given the better survival data. The standardized values in column 2 and 3 merely provide a guide to the proportion of the population surviving (or dying) at each stage. The mortality rate (q_x), that indicates the intensity of mortality, shows that mortality is most intense during the first 12 months of the toad's life history, where q_x = 0.900. Begon and Mortimer (1986) describe k_x as the killing-power within the table. This value indicates that in terms of the regulation of the population size, increases in metamorph output or the survival to the first over-wintering period will have a stronger impact on the size of the adult population than a rise in adult survival. The issues are, however, more complex since the initial number of eggs entering the system is governed by the number of mature females and the although the k_x and q_x values do attempt to describe the intensity of the mortality their effect is inflated, due to the number involved at the juvenile stage.

To be really revealing k_x values are required year on year, however the short length of this study prevents this type of analysis.

Table 8.16: Cohort life-table for the male common toad. The column (a_x) is a summary of the raw data. From the raw data the (l_x) values are calculated representing a standardized figure given 1000 individuals present at the start of the interval. The column (d_x) represents the standardized number dying in each interval. The mortality rate is represented by the (q_x) column, which is adjusted with regard to the numbers in each group. k_x represents the 'killing-power' representing the intensity or rate of mortality.

Age in years *(x)*	Stage	Numbers a_x	Standardized number at the start of age interval x l_x	Standardized number dying between *x* & *x* + 1 d_x	Mortality q_x As a % of the number entering the stage	$\log_{10}a_x$	$\log_{10}l_x$	$\log_{10}a$ - $\log_{10}a$ +1 k_x
0	Eggs	1,125,000	1000	900	0.900	6.051	3.000	1.000
0.3	Metams	112,500	100	75	0.750	5.051	2.000	0.609
1	Juvenile	28,125	25	17.51	0.700	4.449	1.397	0.523
2	Juvenile	8,437	7.49	5.24	0.699	3.926	0.874	0.522
3	Adult	2,531	2.25	1.46	0.645	3.403	0.352	0.454
4	Adult	886	0.79	0.51	0.645	2.947	0.102	0.451
5	Adult	310	0.28	0.18	0.643	2.491	0.553	0.492
6	Adult	108	0.09	0.06	0.666	2.033	1.045	
7	Adult	37	0.03					

Chapter Nine: General discussion

9.1 Introduction

Previous research on amphibian ecology has emphasised the importance of the breeding site in predicting amphibian presence (Chapter 1); research on the terrestrial ecology of the toad has concentrated on the landscape features that predict amphibian presence and the carrying capacity of habitats utilised by toad expressed in terms of habitat densities (Chapter 2). The aim of the current study was to explain the variation within an established population in terms of habitat use. This aim has been approached through a series of field population, studies linked with radio-tracking and field experiments. Denton and Beebee (1993a) compared the density-related features of separate natterjack toad populations in contrasting habitats, showing density-related features in growth, individual condition and foraging strategies. Denton and Beebee's multi-site approach, by their own admission, reduced the ease of identifying variation due to the characteristics of individual populations and those attributable to the variable density and supposed habitat quality. The current study has concentrated on a single population in an attempt to reduce these difficulties, and enable the assessment of the impacts of habitat use. Despite the advances in knowledge of the terrestrial ecology of the toad, the current study possibly represents the first evaluation of the impact of habitat use on the dynamics of the common toad based on the intensive study of a single population. Reading and Clarke (1995) provided an evaluation of the of annual variation in climatic conditions on animal condition, but stated the need to consider the impact of habitat. The current study aims to provide an initial answer to this need.

The following chapter reviews the major results from Chapter 6, 7 and 8, addressing the specific objectives of the current study as outlined in Chapter 2. The results are used to provide an outline description of the habitat requirements at the juvenile and adult stages of the toad's life history.

9.2 Proposed habitat requirements

9.2.1 Juvenile stage

At Osbaston Hall the mean mass of metamorphs emerging from any side of the lake showed some variation, with metamorphs emerging from Lake West (LW) generally smaller than metamorphs emerging on other banks (see Chapter 8). Previous research on the chorus frog (Smith 1987) and common frog (Cummins 1989) has indicated that small metamorphs remain inferior in size to animals emerging at larger sizes throughout their adult lives. However, despite this and the previous observation on the variation in the size at emergence, pitfall trapping failed to establish any particular trend in the spatial variation in adult size due to location of metamoprh emergence (Chapter 6). Indeed, some of the largest adults were caught at the Spinney, to the west of the breeding site.

Juveniles will be able to exploit a larger variety of appropriate refugia than adults, and therefore habitats with little cover may also provide some suitability for juveniles, although they may be more prone to desiccation and thus may require damper habitats or less exposed areas. Deciduous woodland where a thicker ground cover is available will be more suitable than arable fields. Although, evidence suggests that variation may exist between the nature of woodland ground cover. Comparison of juvenile growth rates in the Rookery and Poplars, undertaken at Osbaston in summer 1994, showed that over a period of 125 days juveniles placed in $6m^2$ enclosures grew more rapidly in the Poplars than in the Rookery habitat. Density was equivalent at 0.6 juveniles/m^2. At the end of the experiment there was a 14% difference in juvenile mass. Evaluation of the structure of each habitat (Chapter 7) showed that the Rookery was more limited in groundcover than the Poplars and maybe it is this layer that influences the suitability of habitats for juveniles. At Little Wittenham data (Latham, Bruce and Oldham 1995) showed that juveniles from coniferous plantations were significantly smaller (3.0 +/- 0.5g) than those caught from the deciduous blocks (4.79 +/- 0.7g). Comparison of the habitats at Osbaston and Little Wittenham also appears to suggest that the important ingredient for juveniles is a dense groundcover; the conifer plantation being impoverished in ground vegetation when compared to the

deciduous areas. However, woodland habitats were of higher value for juveniles that other habitats.

It is proposed that home-ranges are established during the first summer spent as a juvenile, post-metamorphosis, this being governed largely by the over-wintering location of the metamorph (Chapters 7 and 8). It is clear that adult toads show a high level of fidelity to etsablished home-ranges (Chapter 7). The position of this over-wintering site is accidental and established through the emergence from the breeding pond. On emergence from the pond it is believed that the toadlet moves out into the surrounding habitat at right angles to the pond edge and will continue to move until autumn temperatures force a decrease in movement (Oldham and Swan 1991). This over-wintering location will form the home-range of the toadlet in subsequent years.

This non-specific form of habitat selection is referred to as *Titania's Syndrome*, where habitat selection is a chance process, based upon the pattern of random dispersion from the breeding pond after emergence. Davis and Krebs (1991) provide the theory of optimality to describe animal habitat selection, based on the ability of any habitat to provide the necessary requirements for survival for a given species. Under optimality an animal will select the habitat that best matches its requirements. In a scenario where an equal number of toadlets emerged from around the perimeter of the breeding site, optimality theory would suggest that a toadlet would disperse until a quality[1] habitat was found; it would be unlikely that a toadlet would remain in an unsuitable habitat. In a fragmented landscape, like Osbaston Hall, the opportunity to select this type of quality habitat may not occur, given migration abilities and landscape form. Since the distance achieved by a toadlet prior to winter is partly governed by weather and habitat conditions, movements will continue until a drop in temperature causes over-wintering and partly by the ease of locomotion through the available habitats.

It has not been possible to establish the reasons for this variation, although increased

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[1] Defined here as possessing suitable characteristics beneficial for the toad.

cover will afford improved shelter from the predation and climatic variation, and may also provide a richer source of food. However, what is clear is that those emerging in the vicinity of deciduous woodland will have a clear advantage over those emerging in the vicinity of poorer habitats. Should the latter survive, however, evidence through recapture data suggest that the toad will maintain this home range in subsequent years, despite the accessibility of other quality habitat. It appears that in this case familiarity with a habitat appears to be of greater importance than the nature of the habitat *per se* in terms of habitat selection, thus explanations of use may not solely be based on an assessment of habitat quality.

Although it is assumed that there is likely to be a difference in the survival of juveniles between habitats of varying quality, based on the assumption that smaller slower growing juveniles are less likely to reach adult status than faster growing individuals (Cohen and Alford 1993). This differential appears to have less regulatory force at Osbaston than the annual variation in the output of metamorphs. During the course of the current study there was variation in the output of metamorphs and it is believed that this had a controlling effect on the adult population size.

9.2.2 Adult stage

9.2.2.1 Habitat quality

Chapters 6 and 7 showed that the proportion of the total catch from the arable traps reflected a consistent density for the arable areas over the course of the current study. This consistency suggests that the arable areas were studied at their carrying capacity for adults, which was low enough to be unaffected by the variation in the input of juveniles. Alternatively, the woodlands were more influenced by the fluctuation in breeding success, due to their higher adult carrying capacity.

Variation in the age at maturity between the male and female will produce a lag between the observed impact of any breeding failure and decline in adult population; breeding failures would be illustrated first in the male population within 2-3 years and in the female over the period 3-4 after the breeding incident. Tracing the impact of

variation in breeding success is further complicated by a lag caused through differences in the age at first breeding (woodland females *viz a viz* arable females, Chapter 8), considered to the result of differences in habitat quality.

Over the course of the population studies at Osbaston, adult male survival in woodland habitats was over twice that observed in the arable areas (Chapter 8). In turn, woodland habitats supported four times the density of adults recorded in arable habitats (Chapter 7). Growth for both sexes was slower in arable areas, resulting in some animals, generating from arable areas, requiring an additional year as a juvenile prior to first breeding. This confirms the importance of semi-natural vegetation within the home range of the toad as indicated by Swan (1986). Habitats typified by a high structural diversity (dense scrub and woodland) are considered to offer a more beneficial habitat to adult toads than areas with limited structural diversity (heavily grazed grassland, arable fields). The ground cover and canopy offered by a woodland provides cover from predation, leaf litter for shelter and a food source. Within a general classification of woodland, areas where there is only limited ground vegetation (e.g. coniferous woodland) is considered to be of less benefit to adults toads.

Dense vegetation was shown to be the most popular refugium site for toads during the current study and animals would hide-up above ground for periods as long as 14 consecutive days. In arable fields, where there was limited basal vegetation and limited hiding material, predation was higher than in the woodland areas, although surface refugia were still used.

9.2.2.2 Distance from breeding site

Adult density at Osbaston Hall was negatively correlated ($r = -0.588$, $p < 0.01$) with distance from the breeding site (Chapter 7), showing a progressive decrease in density away from the breeding site. Density was highest in the Poplars (960-1530 adults/hectare) located 25m from the natal pond. The adult density estimated for the Wood HSE was 205-630 adults/hectare and at the Spinney drift fence was 40-140 adults/hectare. Both of these woodland blocks were surrounded by arable fields, with the Wood located 175m from the pond and Spinney located 400m from the pond

(Chapter 7). In contrast to the fragmented nature of the habitats at Osbaston, data from 1994 and 1995 at Little Wittenham, indicated that the adjusted adult density was consistent, or even increased with distance, within a homogeneous woodland block to a distance of 300m from the pond (Chapter 7). Toads were still caught at this site at distances over 300m on the edges of the homogeneous habitat blocks and migrating from areas of presumed inferior habitat (Chapter 7).

Comparison of the estimated densities at Little Wittenham at similar distances from the breeding site to the Spinney at Osbaston shows that densities are lower than expected. It is hypothesised that this is due to habitat fragmentation, and a result of the intervening arable field, possibly increasing the mortality of newly metamorphosed animals. Thus the 'input' of new animals into these isolated blocks of quality habitat is reduced, and this reduced level is maintained throughout the age classes.

9.2.2.3 Habitat availability

Oldham (1985) suggested that distances of c. 1km could be achieved by a newly metamorphosed toadlet prior to its first over-wintering period. Given this any habitat within 1km can be regarded as available habitat for the toad. For the crested newt Oldham (1994) concluded that blocks of quality habitat (woodland, scrub) within c. 250m of the natal pond were of greater value to the newt than similar blocks at more distal locations. Fragmentation of the habitat may reduce the potential quality by reducing availability (as discussed in the previous section). Although, there was no evidence to suggest that arable fields formed an exclusive barrier to migrating toads at any age class, since even metamorphs were observed to cross arable fields even after harvesting, survival is reduced in habitats considered to be poorer. In contrast, within a relatively homogeneous landscape of quality habitat, as illustrated at Little Wittenham, toad density appears to be consistent throughout the surrounding woodland blocks.

Despite the availability of high quality habitat to a depth of 300m from the pond at Little Wittenham, toads migrated to over-wintering locations outside the band of prime habitat. Migration to over-wintering locations over 400m from the breeding pond was

recorded at Osbaston. For the case of the Osbaston where the Spinney isolated from the pond by 300m of inferior habitat the adult densities were higher than the surrounding arable areas, but lower than that expected for a woodland site. Although fragmentation may have the impact of reducing the total availability of quality habitat, through the increase of mortality and increase predation risk, there is no clear evidence to suggest that the maximum distance for migration is controlled by the availability of quality habitat.

9.2.2.4 Habitat quantity

An attempt was made to estimate the size of the male populations at both study sites. At its peak, the population at Osbaston was estimated to be in the region of 3000 males (with an estimate of c. 3600 including females, section 8.5.1). Within the 30ha Osbaston Estate, there was 4.6ha of woodland with c.300m of the natal pond and a similar area of rough pasture (4ha). The remaining habitat was arable or improved pasture (i.e. formal lawns). Providing a density of 120 adults/hectare. At Little Wittenham a population estimate of 3312 ± 1445 (with an estimate of c.5000 ± 1500 including females) was made in 1995. Given a similar catchment area of c. 300m around the natal pond, the adult density for the Little Wittenham breeding site was estimated to be 170 adult/hectare. The density of adults estimated for the deciduous woodland blocks showed some consistency at each study site and thus the difference in total population size may be attributable to the higher quantity of quality habitat within 300m.

To develop a clearer understanding of the factors involved in explaining habitat densities further research is required in determining the factors that contribute to habitat quality so that predictions may be made and tested. Previous research on winter pheasant density in woodland (Robertson, Woodburn and Hill 1993a, Robertson *et. al.* 1993b) developed a model of predicted densities through stepwise regression and principal component analysis based on studies at 13 sites. Similar studies on the toad could be progressed to help establish the factors affecting density and the impacts of habitat change.

9.2.2.5 Population variation

The original hypothesis was to suggest that adult population would remain stable given consistent environmental conditions. The density estimates for the arable habitats remained consistent over the period of current study, and this was attributable to the relatively low carrying capacity of this habitat dictating the maximum density. The densities estimated in the woodland habitats were higher and more variable. This was, in part, attributed to the changes in the larval output and reciprocal impact on the of the adult population. It was concluded that the woodland habitats were working below their carrying capacities.

The objectives of this study were to evaluate the role of terrestrial habitat, and therefore aquatic condition were not addressed. Given the obvious role of the aquatic environment in metamorph success, this omission has made it difficult to explain the inter-year variation in breeding success given the lack of information on resource availability within the aquatic environment. Regardless to say in this example, it appears that metamorph success was an important role in shaping adult population size. Beebee, Denton and Buckley (1996) found that average population density was positively correlated with toadlet production over the previous decade at their study sites. Interestingly, they concluded that metamorph success rates were dependent upon stochastic rather than density-dependent processes operating at the level of the breeding pond. The short period of the current study (1991-1994) did not permit detailed analysis of the relationship between breeding success and breeding population, however night breeding counts were high in Spur during each of the study years (Chapter 6), yet metamorph output was low (Chapters 6 and 8). Indeed, the size of the Osbaston population appeared to decline over the period 1992-3, yet the metamorph output increased.

9.3 Evaluation of ecological parameters

The final specific objective defined in Chapter 2 aimed to evaluate the use of ecological parameters in defining habitat quality. Selected variables (density, mean age at first breeding, body length, adult growth, condition, survival, home range, sex ratio) used to evaluate habitat quality for the toad population at Osbaston Hall are

Table 9.1: Density-related population parameters for evaluating habitat quality. 1: At first breeding. 2: New animals into the population. 3: % growth/annum. 4: after Kuhn 1994.

	Poplars	Rookery	Arable	Pasture
Density toads/ha	960 - 1530	200 - 430	20 - 70	200 - 380
Mean age[1] **Males** **Females**	 3.8 4.1	 3.5 4.0	 3.2 4.3	 3.2 4.0
Mean DLU (mm)[2] **Males** **Females**	 53.4 ± 0.6 66.2 ± 0.7	 53.5 ± 0.5 64.0 ± 0.7	 53.2 ± 1.2 65.1 ± 0.4	 51.5 ± 0.6 66.2 ± 0.7
Adult growth (males) [3]	1.4-5.2%/year	2.5-3.4%/year	<5.7%/year	Not available
Mean condition[4] **Males** **Females**	 110.2 ± 1.6 127.3 ± 1.6	 107.5 ± 1.7 124.8 ± 1.8	 113.1 ± 1.5 128.1 ± 1.1	 110.9 ± 0.6 126.5 ± 2.0
Survival (males)	34%	32%	14%	15%
Home range (females)	Not available	5602 ± 1472	4161 ± 3064	Not available
Sex ratio	7.6:1	4.6:1	2:1	3.5:1

Proposed grading of habitats using ecological parameters

	Poplars	Rookery	Arable	Pasture
Density toads/ha	1	2	4	3
Mean age[1] **Males** **Females**	 4 3	 3 1	 1 4	 1 1
Mean DLU (mm)[2] **Males** **Females**	 2 1	 1 4	 3 3	 4 1
Adult growth[3]	2	3	1	Not available
Mean condition[4] **Males** **Females**	 2 2	 4 4	 1 1	 3 3
Survival	1	2	4	3
Home range	Not available	2	1	Not available
Sex ratio	4	3	1	2

addressed in Table 9.1. These are discussed in the following sections, in context of the previous sections.

9.3.1 Adult density

Adult density was shown to be higher in the woodland habitats than in the arable habitats; with the pasture areas offering an intermediate density. For Little Wittenham the density was higher in the deciduous former coppice than the coniferous plantation. These data are consistent with those gathered from the literature review (Chapter 1), and discussed in Chapter 8. The original hypothesis is consistent with the results where the density estimates calculated in the current study suggest that woodland can be regarded as of higher suitability than arable.

Density may be used as an indicator of habitat quality, with higher density suggesting a suitable habitat for the target species. Van Horne (1983) questioned this approach, particularly the identification of habitat quality on the basis of summer densities, since this neglected the role of winter habitats. Although, the common toad may select different habitat features for over-wintering refugia than day-to-day summer refugia, these features are, however, likely to lie within the pre-selected home-range rather than represent a new area. A recent study in The Netherlands agreed with this assumption showing that their sample of radio-tagged common toads hibernated in woods and bushes where they were originally captured and released (Bosman, van Gelder and Strijbosch 1996), illustrating the use of summer and winter habitat areas within the same home-range. For this reason it seems appropriate to ignore this initial criticism.

Density could be a mis-leading indicator of habitat quality since it provides 'a moment in time' assessment, especially when it is used without supporting evidence from demographic data, such as survival and other production characteristics. Past events, such as any variations in food source, predation or abiotic environmental factors will influence density, and thus the density observed will not be a reflection of the current habitat quality, rather past conditions. This is of clear importance in the case of the current study, where the variability in density in the woodland habitats is hypothesised

to be a reflection of the changes in the input of metamorphs, whilst the stable densities observed in the arable habitats are considered to be a reflection of the lower carrying-capacity of these habitats which remove the variation in the metamorph input.

9.3.2 Mean length and age at first breeding

The mean length of males caught from the various traps at Osbaston failed to indicate any statistically significant difference between the individual habitats in each year (Chapter 6), except in 1992 where the largest males were caught at the Spinney (SP) and Arable North (AN), and the smallest animals were caught in the central Poplars enclosure (PPI). It was concluded that a minimum length must be achieved prior to breeding and once adult status has been achieved growth declines.

It was hypothesised that toads using predominantly woodland habitats would be younger at first breeding than toads that spent their juvenile period in arable habitats, since growth rates were considered to be slower in arable habitats. The current study indicates that from the sample of new breeders, the mean age of female toads generating from the arable areas was older than those from woodland habitats (Table 9.1), although the modal age for females was four years of age for both habitats (Chapter 8). Analysis of the age distribution in habitats hypothesised to be poorer (i.e. arable) showed a higher percentage of animals as first time breeder in older age groups than in the habitats deemed to be of higher quality (Chapter 8).

This analysis was only completed for females, since it was considered that females would express any variation in habitat quality more than males (Chapter 2). For males, the same pattern was not evident with the mean first time breeding age being higher for animals caught in the Rookery and Poplar Habitat Specific Enclosures (HSEs) than those animals caught at the Arable North drift fence.

Augert and Joly (1993) explained the differences in body size at breeding for adult common frogs at two sites, situated in similar habitats in southeast France, by a longer development period for the larger frogs. For the current study it appears that adult appears to be more strongly by exposure to the terrestrial environment, than the size

at metamorphosis. However size in itself should not be considered as a good reflection of habitat quality since female toads appear to delay breeding if a minimum size has not been achieved in the anticipated year. The rate of growth was seen to slow during the juvenile stage and particularly during adulthood. Delay in achieving adult status provides a longer period at a higher growth rate. For females it appears that the hypothesis was correct, with toads in poorer habitats showing an a higher age at first breeding. For males the reverse was shown, however, the same level detail in analysis between the two contrasting habitats was not carried out for the males.

9.3.3 Annual growth

Individual growth was estimated to be greatest during the first two years after emergence (Chapter 8) and declines once first breeding has occurred. It may therefore be assumed that the habitat the individual is exposed to in the first two years of its life may have the biggest influence on its demographic history. Juvenile growth appeared to be higher in the Poplars compared to the Rookery, given a uniform density. For adults, the growth rate was more consistent in the Rookery.

The delay in first-time breeding for some of the females from the arable habitats at Osbaston suggests that they had not achieved a sufficient size to make breeding viable. In the subsequent year it is suggested that females had reached a sufficient size for breeding to be viable, but were larger than the first time breeder from other habitats. This interpretation is in line with the original hypothesis that growth would be slower in arable habitats

9.2.4 Mean condition

It was suggested in Chapter 6 that males may breed whatever their condition, indicating that, for males, condition is a poor indicator of habitat quality. On the other hand, no significant variation was shown in the body condition of females caught in habitats assumed to be of very different quality, and it was suggested that females in poor condition do not therefore breed. This hypothesis cannot easily be proved in the field, as the trapping methodology collected only toads migrating to the pond during the breeding season in high numbers, so non-breeding females (if they existed) would

not be trapped. Should the assumption that only females in good condition breed be valid, then a minimum viable condition might exist and this would be consistent between different habitats.

For both sexes the use of condition as a means of indicating habitat quality cannot easily be applied in the current study.

9.2.5 Survival

Data from Osbaston Hall over the period 1991-1994 clearly indicated a grading of agricultural habitats that was in line with the quality estimate indicated by adult density. Survival was highest in wooded habitats and lowest in arable habitats. Annual survival is a valuable parameter for habitat studies.

9.2.6 Home range

Home range estimates are provided for radio-tracked individuals in the Rookery and for those released into arable field to the west of the breeding site. The size of the home-ranges were not significantly different and failed to indicate variation that may help to establish any difference in habitat quality. However, the low sample size (n = 12) casts doubt on these conclusions, further work is obviously necessary.

9.2.7 Sex ratio and age at first breeding

Female toads normally take an extra year to reach maturity over males, this delay in maturity is reflected by the sex ratio observed in most toad populations. The sex ratio is therefore an potential parameter to evaluate habitat quality; a low ratio (closer to 1:1) would indicate early maturity by the female and high survival.

The delay in first breeding for females over males is believed to be due to the requirement for growth. Larger size in females is advantageous since larger body size provides a greater maximum viable fecundity (Chapter 8) and is beneficial in breeding. Females located in a quality habitat, that could provide sufficient resources for both growth and egg production, would grow faster and mature earlier than those using inferior habitats. Indeed, comparison of the age distribution of females caught in the

arable traps with those from the Rookery showed a higher number of first year breeder in older age-classes. However, results presented in Chapter 8 showed that the sex ratio from the Poplars and Rookery was over twice those observed in arable habitats. The observed sex ratio in the habitats listed in table 9.1 is confused by the distinct differences in the selection of over-wintering habitat by the common toad. Male toads over-winter in locations closer to the pond than female toads (Chapters 6, 7 and 8) and this may mask any potential relationship.

9.2.8 Fecundity

Fecundity has been correlated with snout to urostyle length producing a weak linear relationship, illustrated by larger females producing more eggs in other studies (Davis and Halliday 1977, Gittins, Kennedy and Williams 1984, Banks and Beebee 1986). In the current study fecundity was also strongly correlated to the body size of females. At Osbaston and Little Wittenham, the high level of variation in fecundity observed within the size classes in comparising these data with other studies, suggests that other forces may be influencing egg production. Unfortunately, there was insufficient data to compare the fecundity of individuals from contrasting habitat as was hoped. Although, body condition was negatively related to fecundity, that might suggest a pressure on resource availability and a balance between egg production and stomatic condition. Indeed, Beebee and Banks (1988) indicated that animals under extreme conditions were more fecund at small sizes than similar animals in improved habitat conditions.

It seem clear, however, that there is a maximum obtainable fecundity controlled by the physical size of the individual and a minimum fecundity, below which it is suggested that females do not breed.

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APPENDIX 1, 2, 3,

Appendix 1

French, J., Latham, D.M., Oldham, R.S. and Bullock, D.J. (1992). An Automated Radio-tracking System for use with Amphibians. *In* Wildlife Telemetry: Remote monitoring and tracking of animals. Chapter 53 477-48. *Ed.* I.G. Priede and S.M. Swift. Ellis Horwood, Chichester.

Appendix 2

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Appendix 4

Trap details 1992-1994

Osbaston terrestrial interception fences 1992-1994

Drift fences

Drift fences were constructed on the edges between distinct habitats.

Functional 1992-1994

Spinney: Length 100m with 10 traps on the wood side and 5 on the field side.
Arable West: Length 100m with 9 traps on the field side.
Arable North: Length 150m with 13 traps on the arable side.

Circular enclosures

Circular enclosures have been used in previous studies (Oldham 1966, 1967) and have the advantage of simultaneously providing information on dispersal, orientation and habitat density. The circular enclosures at Osbaston were designed with a short 2 metre arm on the outside edge of the fence; these were intended to increase the trapping area and therefore help increase trapping numbers.

Functional 1992 (only)

Rough Wood: Length 70m with 10 traps on the wood side and 6 on the field side.
Rough Field: Length 80m with 4 traps on the rough side and 5 on the lawn side.
Rough Inner: Length 80m with 11 traps on the inner side.

These fences formed the **Rough East** complex together with the hedge that divides the rough pasture and arable field.

Functional 1991-94

Rookery: Radius of 30m and 198m circumference, 20 pitfalls on the inside and 12 pitfalls on the outside towards the south-east.
Poplars: Similar radius to the Rookery with 20 pitfalls on the inner arc and 12 on the western half of the circle, facing the Arable West drift fence.

Smaller circular enclosures were constructed in 1993 and 1994 in the poplars and used as part of the fence evaluation trials.

Habitat specific enclosures

Functional 1992 (only)

Wood: A 380m fence length around a wood 28 pitfalls on the inside with 15 pitfalls on the outside (field).

Functional 1992-94
Hedge: Length of 160m divided into three sections; Hedge Centre, Hedge North, Hedge East. 8 pitfalls within each of the hedge sections.

Functional 1994 (only)
Arable hedge: The hedge running from the north-west tip of the lake to the spinney was divided into three 50 metre hedge enclosures each containing eight pitfalls.

Appendix 5

Error histograms for bearing estimates

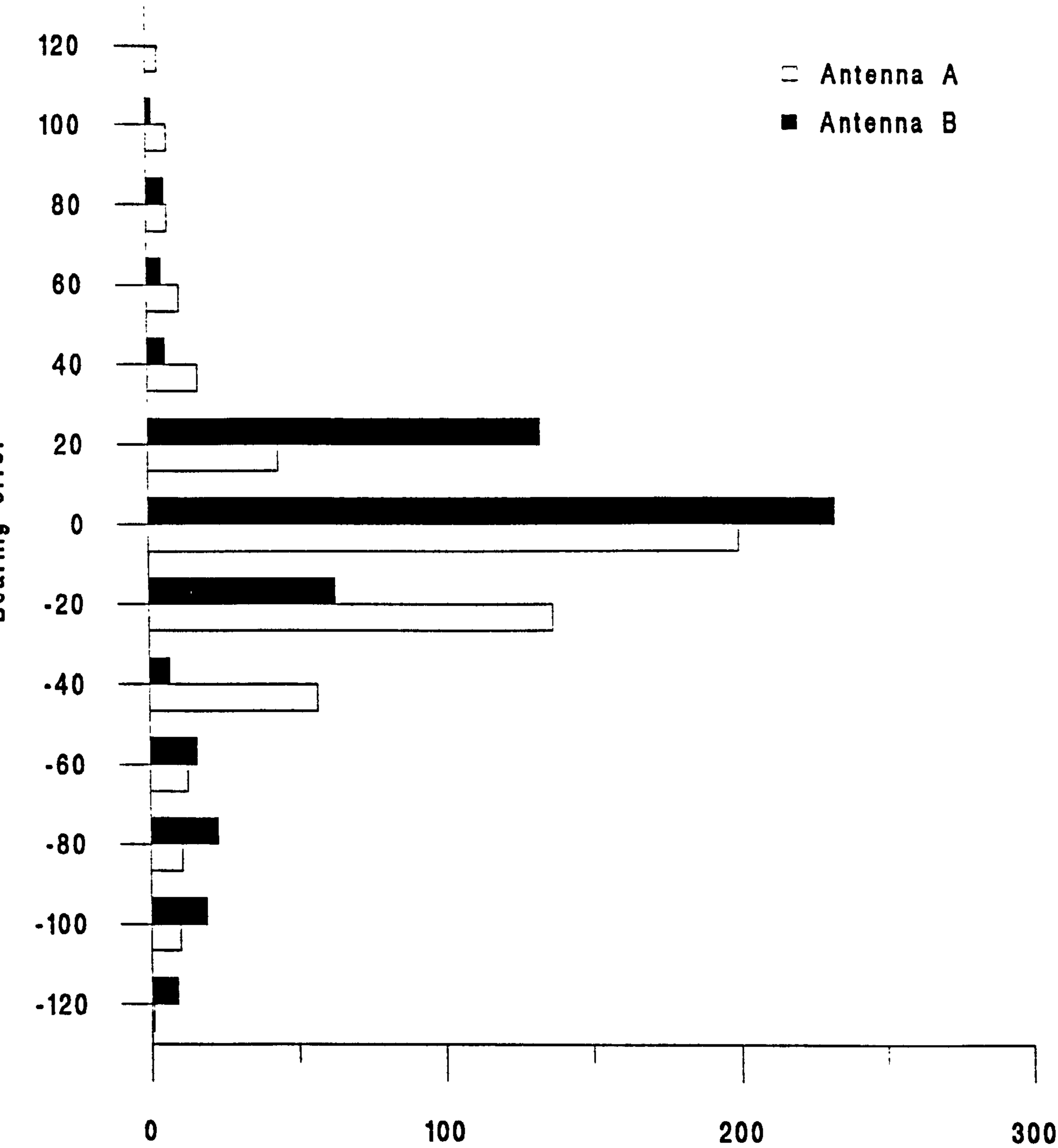

Figure 1: Distribution of the error bearings for the Coleorton system, with a negative bias shown by antenna A, antenna B free from bias.

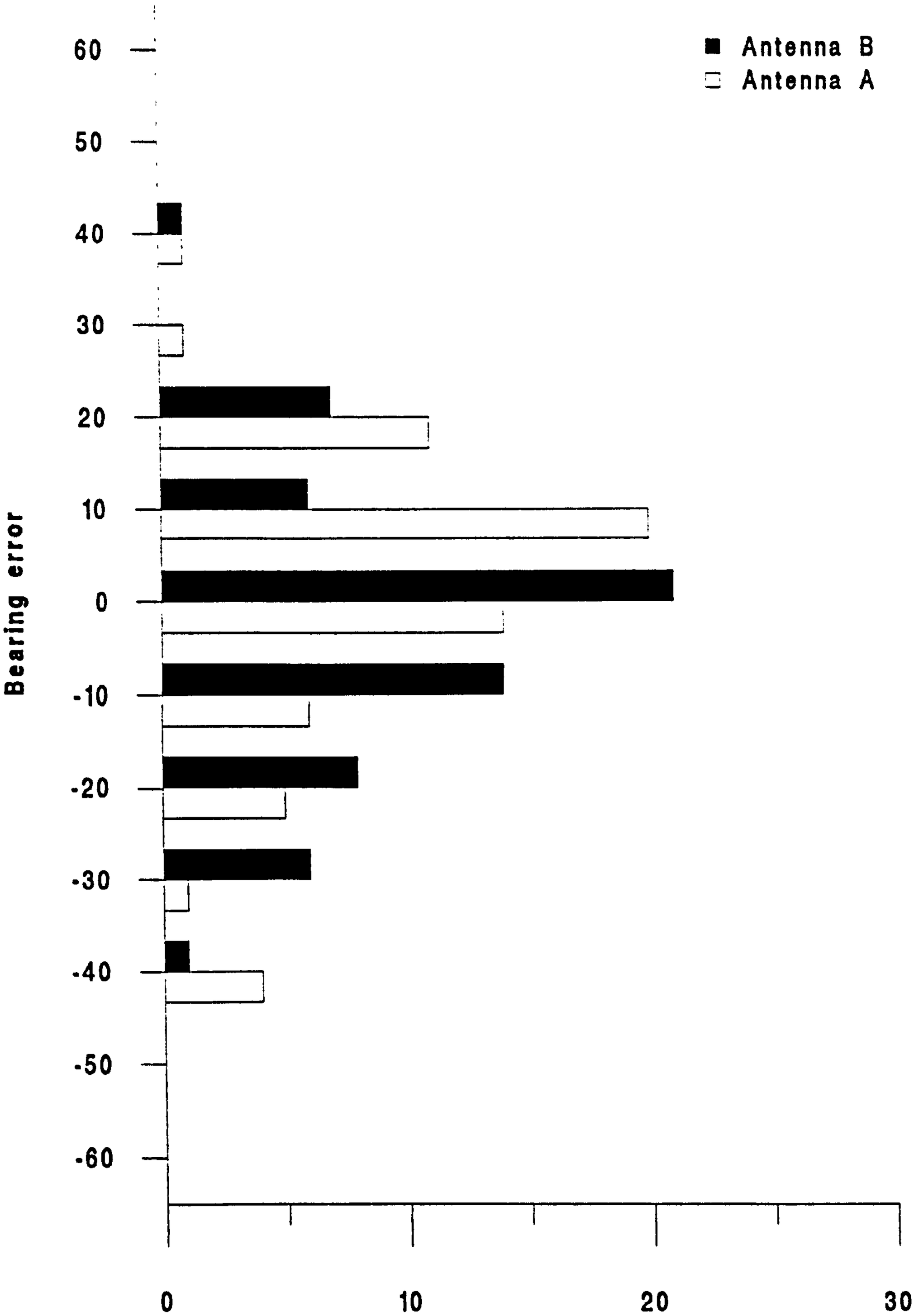

Figure 2: Distribution of bearing errors for perimeter locations, with antennae free from bias.

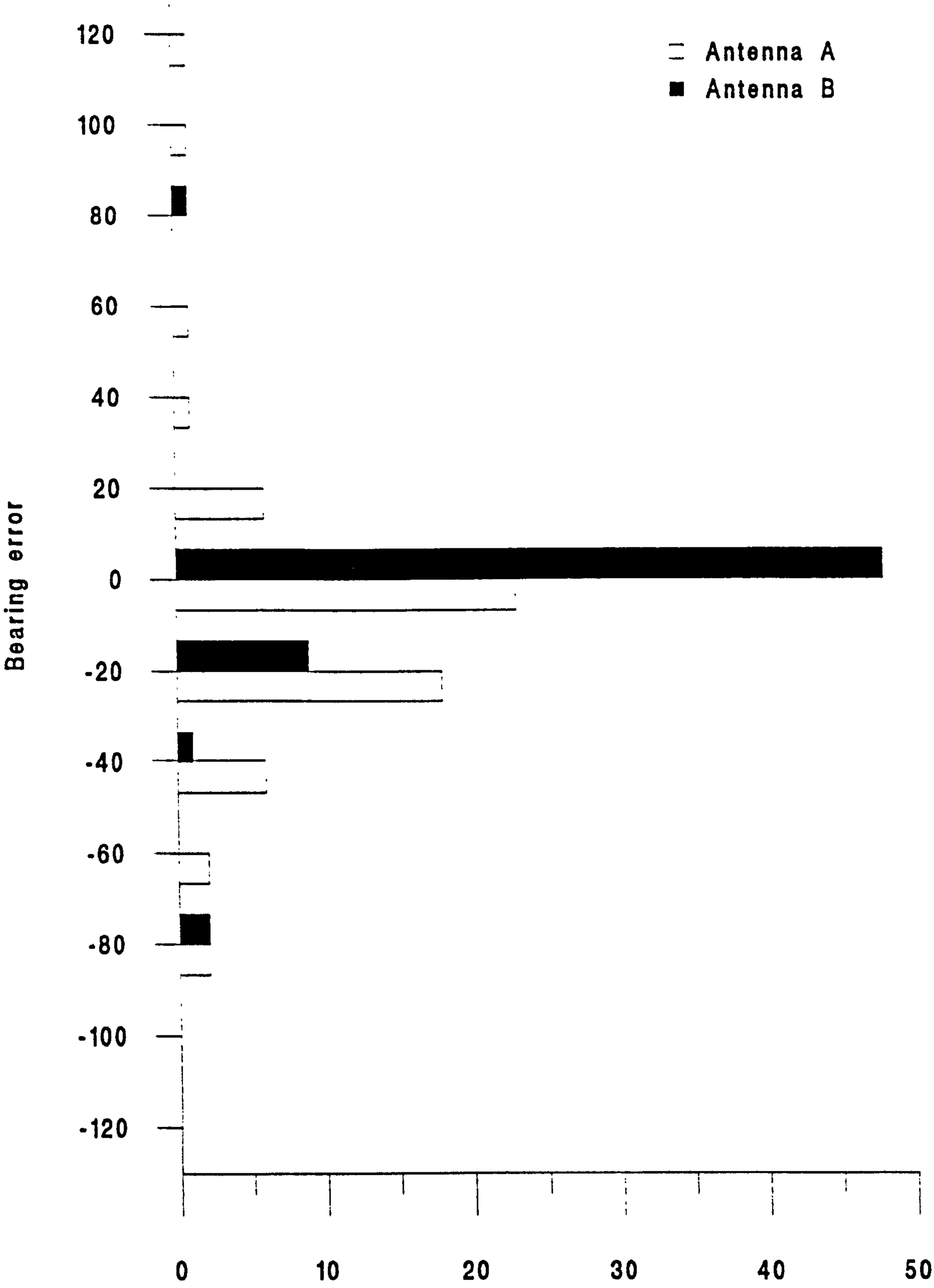

Figure 3: Distribution of bearing errors for locations close to release point. Both antennae with negative bias. Antenna A also illustrating a lower degree of precision than B.

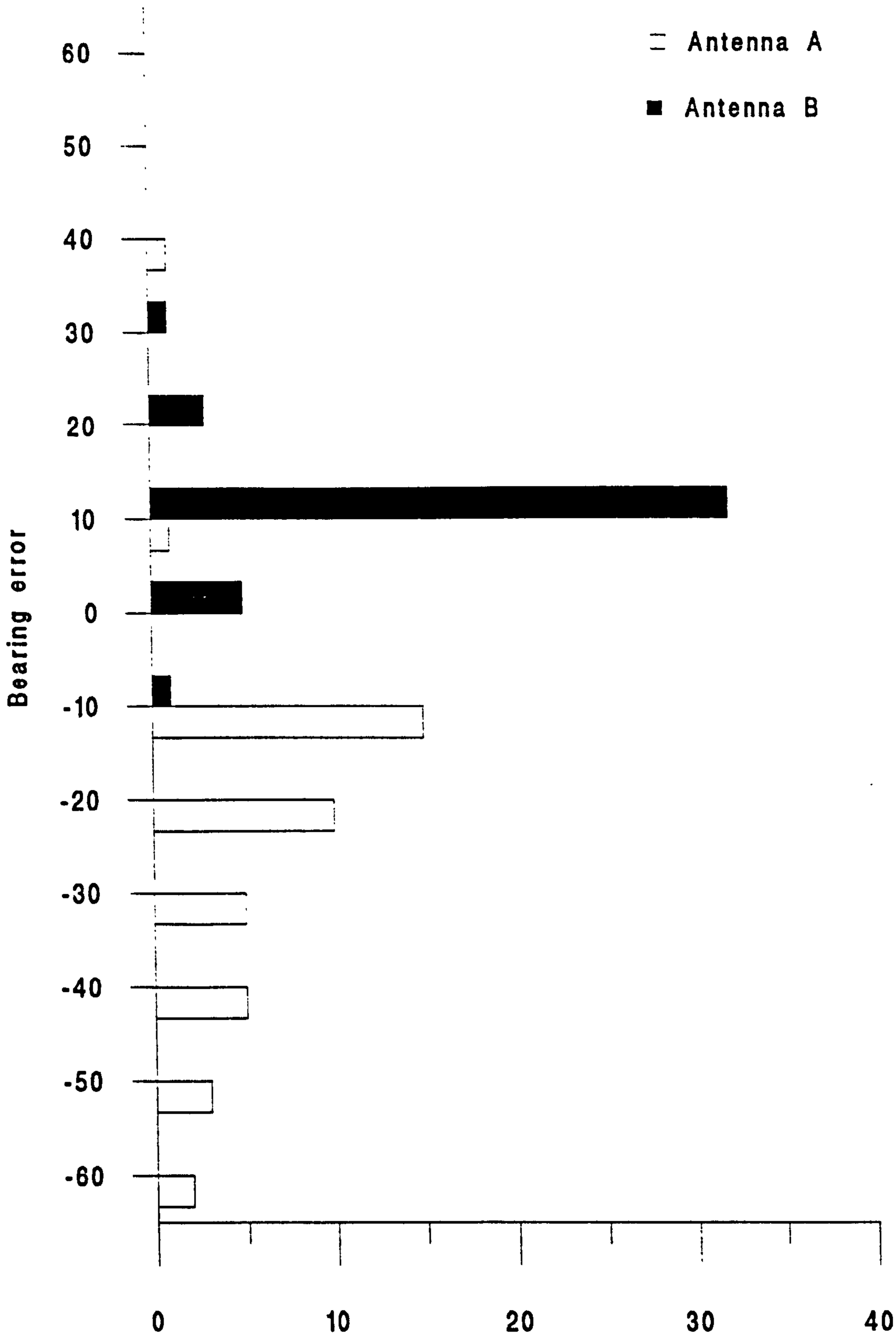

Figure 4: Distribution of bearing errors at location Tree 1, antenna A with negative bias and antenna B with positive bias

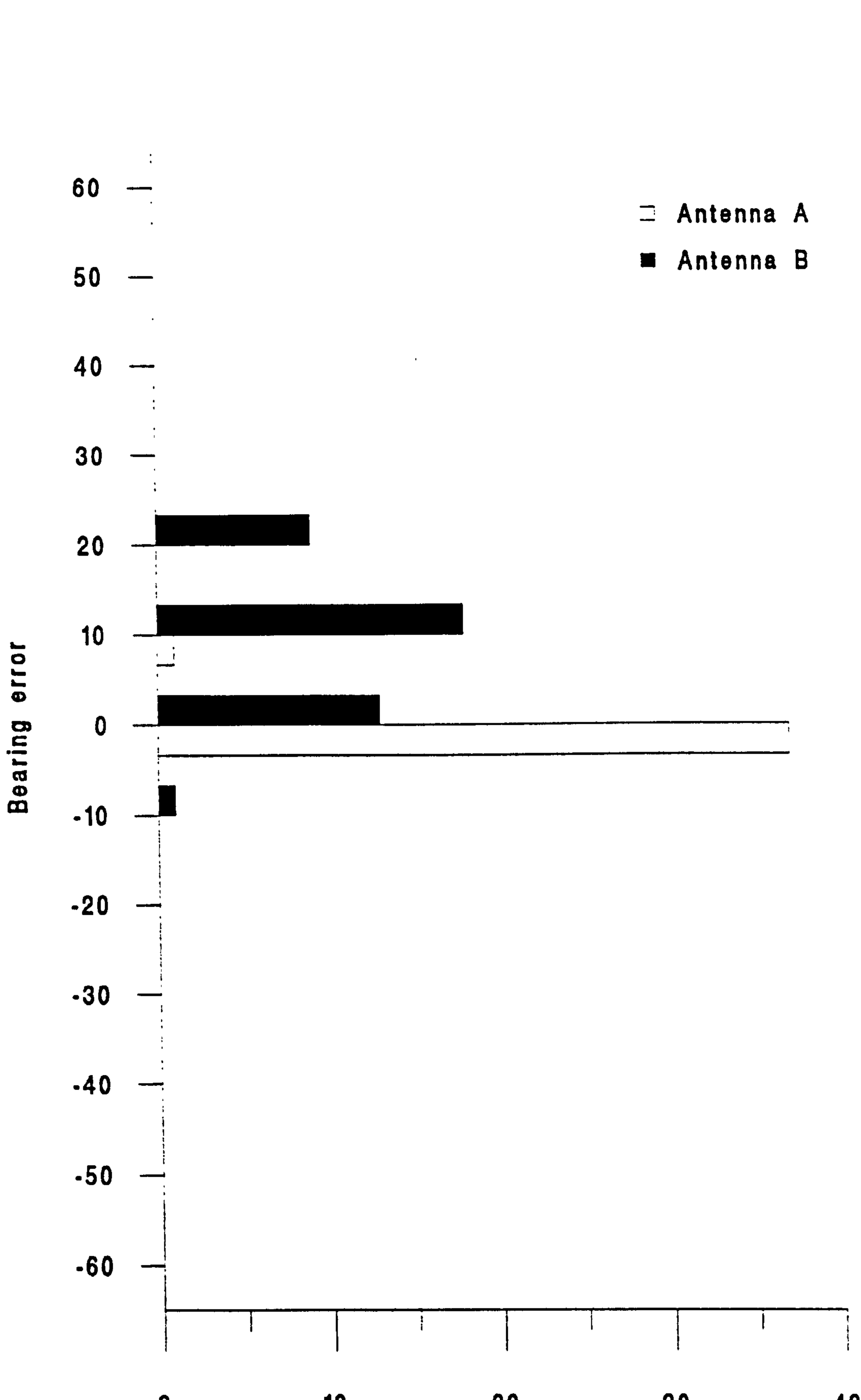

Figure 5: Distribution of beraing errors for Tree 2 location, antenna B with positive bias. Antenna A free from bias.

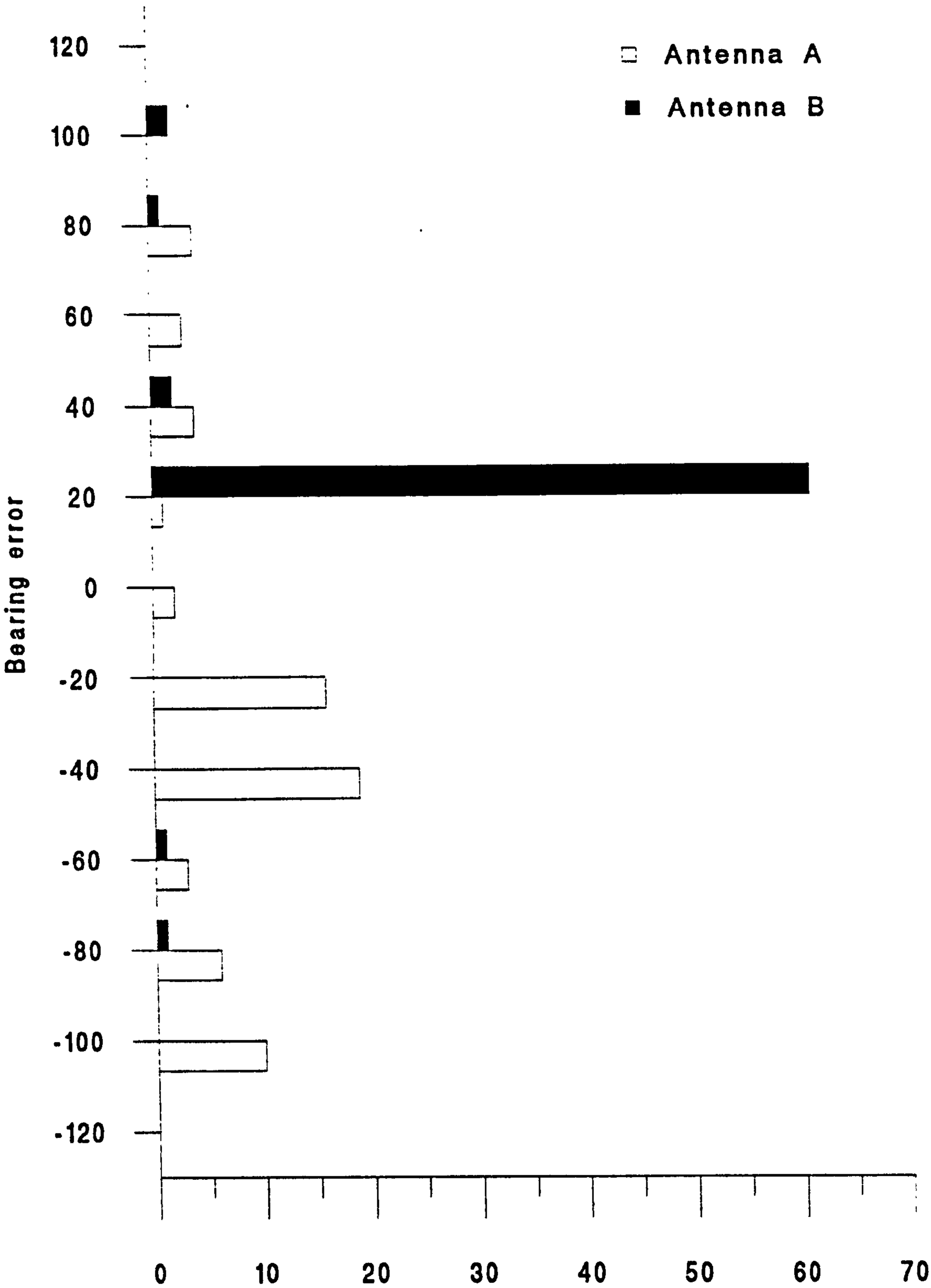

Figure 6: Distribution of bearing errors for tree 3 location, with loss of bearing accuracy by both antennae.

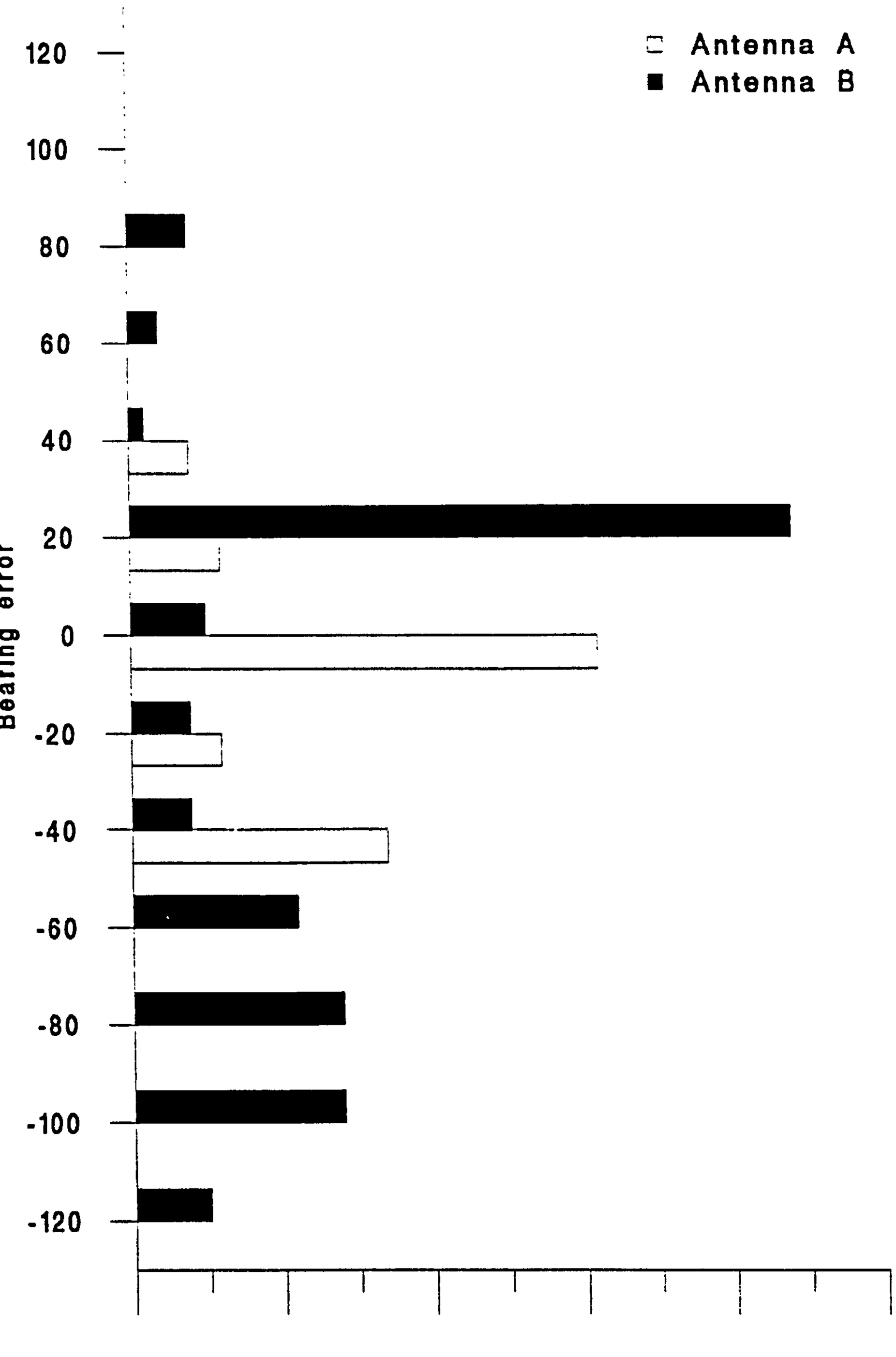

Figure 7: Distribution of bearing errors for tree 4 location, antenna B with slight negative bias. Low precision illustrated by antenna A.

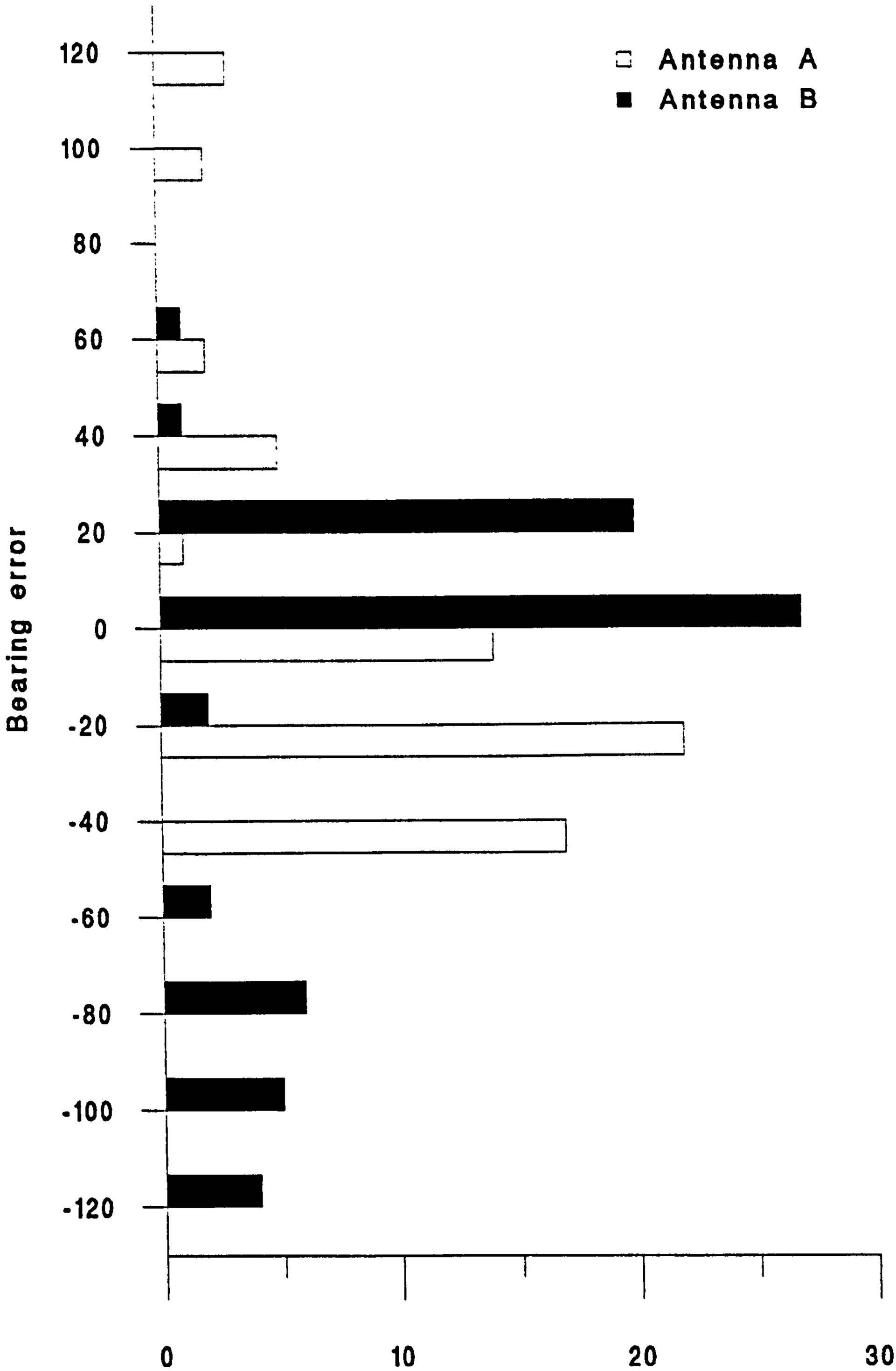

Figure 8: Distribution of bearing errors for tree 5 location, antenna A with negative bias and antenna B with no bias.

Appendix 6

Climatic cues for the spring migration

Toad migrations and weather conditions

There was no consistent correlation with the day of the year and catch, Table 1. The correlation between daily catch and *Maxtemp* was significant in 1992 and 1993 and proved to be the only significant variable amongst those tested in the combined data set representing the full three years ($r = 0.435$, $p < 0.01$), Table 1. The correlation between daily catch and *Mintemp* was significantly only in 1993. The remaining variables of *rainfall*, *windspeed* and *sunshine hrs* were not shown to have significant influence individually on daily toad catch.

Stepwise multiple regression was used to describe the relationship between climatic factors and select the optimal subset of variables, Table 2. In 1992, the full set of climatic variables (*maxtemp, mintemp, rainfall, windspeed, sunshine hrs*) explained 50.1% of the variation in the daily toad catch from the pitfalls (R^2-adjusted). The subset *(maxtemp, windspeed, sunshine hrs, rainfall*) improved the best-fit model to 99.6%. In 1993, the full set of climatic variables explained 95.2% of the variation, with the optimum set (*windspeed*, maxtemp, mintemp, sunshine hrs) barely increasing this value. The data from 1994 were unusual in comparison with previous years, providing a very low R^2-adjusted value for the optimal subset of only 8.1% (*rainfall* and *windspeed*).

In a combined data set, representing 1992-1994, the full set of climatic variables (*maxtemp, mintemp, rain, windspeed and sunshine hours*), explained 14.1%, with the optimal subset (*maxtemp, sunshine hours and windspeed*), providing a slightly increased value of 18.4%.

TABLE 1: Product moment correlations for the number of toads caught in the terrestrial traps with climatic conditions obtained from details in the Leicester Mercury. * significant p = 0.05, ** significant at p = 0.01.

Climatic variable	1992	1993	1994	All years
Maxtemp	0.540*	0.593*	0.215	0.435**
Mintemp	0.205	0.560*	0.249	0.223
Rainfall	0.034	-0.241	0.382	0.102
Windspeed	0.347	0.427	0.237	0.191
Sunshine hrs	0.084	-0.143	-0.281	-0.120
Date	0.160	0.242	0.282	0.238

TABLE 2: Comparison of R^2-adjusted values (in %) obtained in linear regression with the daily toad catch.

	1992 (n = 17)	1993 (n = 9)	1994 (n = 13)	All years (n =39)
Full set of climatic variables	50.1	95.2	0	14.1
Optimal subset *	99.6	95.3	8.1	18.4
* Optimal subset in descending order of significance	*Maxtemp* *Wind* *Sunshine hours* *Rainfall*	*Wind* *Maxtemp* *Mintemp* *Sunshine hours*	*Rainfall* *Wind*	*Maxtemp* *Sunshine hours* *Wind*

Appendix 7

Tukey test results (Chapter 6)

TABLE 6.1: Tukey test results for comparison of the male length (DLU) in samples from different habitats in 1992.

Sample	AN	AW	SP	REI	PPI	RKI	HDI	WDI	REF
AW	57.9								
SP	11.9	69.8							
REI	55.8	2.2	67.5						
PPI	32.5	25.3	44.3	23.2					
RKI	33.2	24.7	45.0	22.6	0.7				
HDI	36.7	21.2	48.6	19.1	4.2	3.5			
WDI	56.0	1.9	67.7	0.2	23.4	22.7	19.2		
REF	47.7	10.3	60.3	8.2	15.1	14.5	10.8	8.3	
REW	22.8	35.1	34.6	33.0	9.7	10.4	13.9	33.2	24.9

ANOVA, F = 2.41, p = 0.011.

Tukey pairwise comparisons

Family error rate = 0.0500
Individual error rate = 0.0017

Critical value = 4.47

TABLE 6.2: Tukey test results for comparison of the male condition in samples from different habitats in 1992.

Sample	AN	AW	SP	REI	PPI	RKI	HDI	WDI	REF
AW	2.18								
SP	8.66	10.12							
REI	8.14	5.95	16.08						
PPI	0.58	2.76	7.36	8.72					
RKI	7.55	9.76	0.38	11.55	6.97				
HDI	5.16	7.35	2.77	13.3	4.58	2.39			
WDI	5.55	3.37	13.48	2.59	6.13	13.1	10.71		
REF	8.73	6.55	16.66	0.59	9.31	16.29	13.90	3.18	
REW	2.16	4.34	5.78	10.29	1.58	5.44	3.01	7.70	10.89

ANOVA, F = 2.96, p = 0.002.

Tukey pairwise comparisons

Family error rate = 0.0500
Individual error rate = 0.0017

Critical value = 4.47

TABLE 6.3: Tukey test results for comparison of the male condition in samples from different habitats in 1993.

Sample	PPI	RKI	AW	AN	HDI
RKI	13.77				
AW	17.44	3.66			
AN	22.82	36.6	40.26		
HDI	8.06	21.87	25.5	14.76	
SP	4.15	17.93	21.59	18.67	3.91

ANOVA, F = 2.77, p = 0.026.

Tukey pairwise comparisons

Family error rate = 0.0500
Individual error rate = 0.0046

Critical value = 4.17

Appendix 8

Compositional analysis matrixes for radio-tracked toads (1992)

Matrix of logratio differences between utilized and available habitat compositions for the female 001. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-3.018	-2.883	-1.024	-2.024	
Improved	3.018		0.135	1.994	0.840	
Rough	2.883	-0.135		1.859	0.704	
Wood	1.024	-1.994	-1.859		-1.154	
Hedge	2.178	-0.840	-0.704	1.154		
Cultivated						5
Improved						1
Rough						2
Wood						4
Hedge						3

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.156	0.660	1.500	7.983	
Improved	-1.156		-0.496	0.344	6.827	
Rough	-0.660	0.496		0.840	7.323	
Wood	-1.500	-0.344	-0.840		6.482	
Hedge	-7.983	-6.827	-7.323	-6.482		
Cultivated						1
Improved						3
Rough						2
Wood						4
Hedge						5

Matrix of logratio differences between utilized and available habitat compositions for the female 002. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.609	0.239	1.604	-0.401	
Improved	0.609		0.843	2.213	0.219	
Rough	-0.239	-0.843		1.370	-0.635	
Wood	-1.604	-2.213	-1.370		-2.004	
Hedge	0.401	-0.219	0.635	2.004		
Cultivated						3
Improved						1
Rough						4
Wood						5
Hedge						2

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.534	0.028	-0.029	-0.279	
Improved	0.534		0.562	0.505	-0.236	
Rough	-0.028	-0.526		-0.057	-0.325	
Wood	0.029	-0.505	0.057		-0.268	
Hedge	0.297	-0.236	0.325	0.268		
Cultivated						
Improved						
Rough						
Wood						
Hedge						

Matrix of logratio differences between utilized and available habitat compositions for the male 004. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.857	-0.778	-0.939	-0.677	
Improved	0.857		0.079	-0.082	0.180	
Rough	0.778	-0.079		-0.161	0.101	
Wood	0.939	0.082	0.161		0.262	
Hedge	0.677	-0.180	-0.101	-0.262		
Cultivated						5
Improved						2
Rough						3
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.520	-0.646	-1.150	6.481	
Improved	0.520		-0.127	-0.630	7.001	
Rough	0.646	0.127		-0.504	7.128	
Wood	1.150	0.630	0.504		7.631	
Hedge	-6.481	-7.001	-7.128	-7.631		
Cultivated						4
Improved						3
Rough						2
Wood						1
Hedge						5

Matrix of logratio differences between utilized and available habitat compositions for the female 005. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.956	-3.711	-3.743	6.657	
Improved	0.956		-2.755	-2.787	7.613	
Rough	3.711	2.755		-0.032	10.368	
Wood	3.743	2.787	0.032		10.400	
Hedge	-6.657	-7.613	-10.368	-10.400		
Cultivated						4
Improved						3
Rough						2
Wood						1
Hedge						5

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0	3.28	1.986	0	
Improved	0		0	0	0	
Rough	-3.28	0		-1.294	0	
Wood	-1.989	0	1.294		0	
Hedge	0	0	0	0		
Cultivated						1
Improved						2
Rough						5
Wood						4
Hedge						2

Matrix of logratio differences between utilized and available habitat compositions for the male 006. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-1.429	-1.901	-1.888	-0.650	
Improved	1.429		-0.472	-0.459	0.780	
Rough	1.901	0.472		0.013	1.252	
Wood	1.888	0.459	-0.013		1.238	
Hedge	0.650	-0.780	-1.252	-1.238		
Cultivated						5
Improved						3
Rough						1
Wood						2
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.034	-0.760	-1.661	-1.147	
Improved	-1.034		-1.794	-2.695	-2.180	
Rough	0.760	1.794		-0.901	-0.387	
Wood	1.661	2.695	0.901		0.514	
Hedge	1.147	2.180	0.387	-0.514		
Cultivated						4
Improved						5
Rough						3
Wood						1
Hedge						2

Matrix of logratio differences between utilized and available habitat compositions for the male 007. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.795	0.261	0.024	0.153	
Improved	-0.795		-0.534	-0.771	-0.642	
Rough	-0.261	0.534		-0.237	-0.108	
Wood	-0.024	0.771	-0.237		0.129	
Hedge	-0.153	0.642	0.108	-0.129		
Cultivated						1
Improved						5
Rough						4
Wood						2
Hedge						3

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.889	3.284	0.827	-0.089	
Improved	-0.889		2.389	-0.062	-0.977	
Rough	-3.284	-2.396		-2.458	-3.373	
Wood	-0.827	0.062	2.458		-0.915	
Hedge	0.089	0.997	3.373	0.915		
Cultivated						
Improved						
Rough						
Wood						
Hedge						

Matrix of logratio differences between utilized and available habitat compositions for the female 008. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.394	0.319	-0.442	0.001	
Improved	-0.394		-0.074	-0.835	-0.393	
Rough	-0.319	0.074		-0.761	-0.318	
Wood	0.442	0.835	0.761		0.443	
Hedge	-0.001	0.393	0.381	-0.443		
Cultivated						2
Improved						5
Rough						4
Wood						1
Hedge						3

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.374	0.931	-0.802	0.877	
Improved	-1.374		-0.443	-2.176	-0.497	
Rough	-0.931	0.443		-1.733	-0.054	
Wood	0.802	2.176	1.733		1.679	
Hedge	-0.877	0.497	0.054	-1.679		
Cultivated						2
Improved						5
Rough						4
Wood						1
Hedge						3

Matrix of logratio differences between utilized and available habitat compositions for the male 009. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.076	-0.071	-0.013	-0.076	
Improved	0.076		0.005	0.0063	0	
Rough	0.071	-0.005		0.058	-0.005	
Wood	0.013	-0.063	-0.058		-0.063	
Hedge	0.076	0	0.005	0.063		
Cultivated						5
Improved						1
Rough						3
Wood						4
Hedge						1

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-10.256	-9.707	-7.557	-2.186	
Improved	10.256		0.549	2.679	8.070	
Rough	9.707	-0.549		2.130	7.521	
Wood	7.577	-2.679	-2.130		5.391	
Hedge	2.186	-8.070	-7.521	-5.391		
Cultivated						5
Improved						1
Rough						2
Wood						3
Hedge						4

Matrix of logratio differences between utilized and available habitat compositions for the female 010. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.461	-0.461	-0.432	-0.461	
Improved	0.461		0	0.029	0	
Rough	0.461	0		0.029	0	
Wood	0.432	-0.029	-0.029		-0.029	
Hedge	0.461	0	0	0.029		
Cultivated						5
Improved						1
Rough						1
Wood						4
Hedge						1

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-2.238	-1.164	-0.479	5.992	
Improved	2.238		1.073	1.759	8.230	
Rough	1.164	-1.073		0.686	7.423	
Wood	0.479	-1.759	-0.686		6.738	
Hedge	-5.992	-8.230	-7.423	6.738		
Cultivated						4
Improved						1
Rough						2
Wood						3
Hedge						5

Matrix of logratio differences between utilized and available habitat compositions for the female 011. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.843	-0.110	1.729	-0.653	
Improved	0.843		0.733	2.572	0.190	
Rough	0.110	-0.733		1.839	-0.539	
Wood	-1.729	-2.572	-1.839		-2.382	
Hedge	0.653	-0.190	0.539	2.382		
Cultivated						4
Improved						1
Rough						3
Wood						5
Hedge						2

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.337	2.136	6.908	0.109	
Improved	0.337		2.472	7.245	0.449	
Rough	-2.136	-2.472		4.773	-2.026	
Wood	-6.908	-7.245	-4.773		-6.799	
Hedge	-0.109	-0.446	2.026	6.799		
Cultivated						2
Improved						1
Rough						5
Wood						4
Hedge						3

Matrix of logratio differences between utilized and available habitat compositions for the male 012. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.626	-0.338	-0.432	-0.638	
Improved	0.626		0.228	0.193	-0.013	
Rough	0.338	-0.228		-0.095	-0.301	
Wood	0.432	-0.193	0.095		-0.260	
Hedge	0.638	0.013	0.301	0.206		
Cultivated						5
Improved						2
Rough						4
Wood						3
Hedge						1

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-8.218	-8.436	-9.526	-1.161	
Improved	8.218		-0.218	-1.307	7.057	
Rough	8.436	0.218		-1.089	7.275	
Wood	9.526	1.307	1.089		8.364	
Hedge	1.161	-7.057	-7.275	-8.364		
Cultivated						5
Improved						3
Rough						2
Wood						1
Hedge						4

Matrix of logratio differences between utilized and available habitat compositions for the female 013. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.430	-0.417	0.359	-0.521	
Improved	0.430		0.014	0.789	-0.091	
Rough	0.417	-0.014		0.775	-0.105	
Wood	-0.359	-0.789	-0.775		-0.880	
Hedge	0.521	0.091	0.105	0.880		
Cultivated						4
Improved						2
Rough						3
Wood						5
Hedge						1

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.739	-0.757	0.810	-0.579	
Improved	0.739		-0.018	1.549	0.159	
Rough	0.757	0.018		1.567	0.177	
Wood	-0.810	-1.519	-1.567		-1.390	
Hedge	0.579	-0.159	-0.177	1.390		
Cultivated						4
Improved						2
Rough						1
Wood						5
Hedge						3

Matrix of logratio differences between utilized and available habitat compositions for the female 014. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.188	-0.115	-0.805	-0.072	
Improved	0.188		0.073	-0.617	0.115	
Rough	0.115	-0.073		-0.689	0.043	
Wood	0.805	0.617	0.689		0.732	
Hedge	0.072	-0.115	-0.043	-0.732		
Cultivated						5
Improved						2
Rough						3
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.315	-0.652	1.398	-0.220	
Improved	-0.315		-0.968	1.083	-0.536	
Rough	0.652	0.968		2.051	0.432	
Wood	-1.398	-1.083	-2.051		-1.619	
Hedge	0.220	0.536	-0.432	1.619		
Cultivated						3
Improved						4
Rough						1
Wood						5
Hedge						2

Matrix of logratio differences between utilized and available habitat compositions for the male 017. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.953	-1.781	-1.969	-0.484	
Improved	0.953		-0.827	-1.015	0.469	
Rough	1.781	0.827		-0.188	1.297	
Wood	1.969	1.015	0.188		1.485	
Hedge	0.484	-0.469	-1.297	-1.485		
Cultivated						5
Improved						3
Rough						2
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.423	0.474	-0.956	5.595	
Improved	0.423		0.897	0.533	6.018	
Rough	-0.474	-0.897		-1.430	5.121	
Wood	0.956	0.533	1.430		6.551	
Hedge	-5.595	-6.018	-5.121	-6.551		
Cultivated						3
Improved						2
Rough						4
Wood						1
Hedge						5

Matrix of logratio differences between utilized and available habitat compositions for the male 018. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-10.477	-10.860	-11.744	-1.767	
Improved	10.477		-0.383	-1.268	9.064	
Rough	10.860	0.383		-0.884	8.680	
Wood	11.744	1.268	0.884		9.948	
Hedge	1.797	-9.064	-8.680	-9.948		
Cultivated						5
Improved						3
Rough						2
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0	0	0	0	
Improved	0		1.860	-0.994	0	
Rough	0	-1.860		-2.840	0	
Wood	0	0.994	2.840		0	
Hedge	0	0	0	0		
Cultivated						2
Improved						4
Rough						5
Wood						1
Hedge						2

Matrix of logratio differences between utilized and available habitat compositions for the female 019. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.963	-0.437	-0.464	0.922	
Improved	-1.963		-2.400	-2.428	-1.041	
Rough	0.437	2.400		-0.027	1.359	
Wood	0.464	2.428	0.027		1.386	
Hedge	-0.922	1.041	-1.359	-1.386		
Cultivated		+	-	-	+	3
Improved	-		-	-	-	5
Rough	+	+		-	+	2
Wood	+	+	+		+	1
Hedge	-	+	-	-		4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.310	-0.249	-1.482	-0.383	
Improved	-0.310		-0.560	-1.792	-0.693	
Rough	0.249	0.560		-1.232	-0.134	
Wood	1.482	1.792	1.232		1.099	
Hedge	0.383	0.693	0.134	-1.099		
Cultivated						4
Improved						5
Rough						3
Wood						1
Hedge						2

Matrix of logratio differences between utilized and available habitat compositions for the male 021. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.024	0.198	-0.331	0.427	
Improved	-1.042		-0.843	-1.372	-0.614	
Rough	-0.198	0.843		-0.529	0.229	
Wood	0.331	1.372	0.529		0.758	
Hedge	-0.427	0.614	-0.229	-0.758		
Cultivated						2
Improved						5
Rough						3
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.831	2.438	-2.003	0.331	
Improved	-0.831		1.607	2.834	-0.500	
Rough	-2.438	-1.607		-4.441	-2.107	
Wood	2.003	2.834	4.441		2.334	
Hedge	-0.331	0.500	2.107	-2.334		
Cultivated						2
Improved						4
Rough						5
Wood						1
Hedge						3

Matrix of logratio differences between utilized and available habitat compositions for the male 022. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.319	-0.293	0.652	-0.319	
Improved	0.319		0.026	0.971	0	
Rough	0.293	-0.026		0.945	-0.026	
Wood	-0.652	-0.971	-0.945		-0.971	
Hedge	0.319	0	0.026	0.971		
Cultivated						4
Improved						1
Rough						3
Wood						5
Hedge						1

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.904	3.072	1.137	1.220	
Improved	0.904		3.976	2.042	2.125	
Rough	-3.072	-3.976		-1.935	-1.852	
Wood	-1.137	2.042	1.935		0.083	
Hedge	-1.220	2.125	1.852	0.083		
Cultivated						2
Improved						1
Rough						5
Wood						3
Hedge						4

Matrix of logratio differences between utilized and available habitat compositions for the male 024. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-0.514	-0.638	-0.765	-0.696	
Improved	0.514		-0.096	-0.232	-0.181	
Rough	0.638	0.096		-0.127	-0.058	
Wood	0.765	0.232	0.127		0.069	
Hedge	0.696	0.181	0.058	-0.069		
Cultivated						5
Improved						4
Rough						3
Wood						1
Hedge						2

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-1.942	0	-0.662	-0.662	
Improved	1.942		1.942	1.262	1.280	
Rough	0	-1.942		-0.662	-0.662	
Wood	0.662	-1.262	0.662		0	
Hedge	0.662	-1.280	0.662	0		
Cultivated						4
Improved						1
Rough						4
Wood						2
Hedge						3

Matrix of logratio differences between utilized and available habitat compositions for the female 025. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.125	0.013	-0.223	0.087	
Improved	-0.125		-0.112	-0.348	-0.061	
Rough	-0.013	0.112		-0.236	0.074	
Wood	0.223	0.348	0.236		0.310	
Hedge	-0.087	0.061	-0.074	-0.310		
Cultivated						2
Improved						5
Rough						3
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		1.350	0.187	-2.079	-0.347	
Improved	-1.350		-1.163	-3.429	-1.674	
Rough	-0.187	1.163		-2.266	-0.533	
Wood	2.079	3.429	2.266		1.733	
Hedge	0.347	1.674	0.533	-1.733		
Cultivated						
Improved						
Rough						
Wood						
Hedge						

Matrix of logratio differences between utilized and available habitat compositions for the female 026. The habitat utilisation is shown by replacing each figure by its sign and counting the number of positive value to denote the rank. The row with most positive figures represents the most-used habitat, rank 1.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		0.939	0.015	-1.279	0.230	
Improved	-0.939		-0.939	-2.218	-0.709	
Rough	-0.015	0.939		-1.294	0.215	
Wood	1.279	2.218	1.294		1.510	
Hedge	-0.230	0.709	-0.215	-1.510		
Cultivated						2
Improved						5
Rough						3
Wood						1
Hedge						4

Use of MCP derived from radio-fixed versus MCP area of utilisation.

	Cultivated	Improved	Rough	Wood	Hedge	Rank
Canopy	None	None	None	Open	None	
Ground Cover	Poor	Yes	Yes	Yes	Yes	
Cultivated		-1.161	-1.330	2.440	-1.344	
Improved	1.161		-0.155	3.602	-0.182	
Rough	1.330	0.155		3.770	-0.014	
Wood	-2.440	-3.602	-3.770		-3.784	
Hedge	1.344	0.182	0.014	3.784		
Cultivated						4
Improved						3
Rough						2
Wood						5
Hedge						1

Appendix 9

Tukey test results (Chapter 8)

TABLE 8.1: Tukey test results for comparison of metamorph emerging from each of the banks of the Lake at development stage 0 (i.e. full tail absorption), Osbaston 1992.

Level	North	East	South
East	0.024		
South	0.036	0.372	
West	0.189	0.018	0.032

ANOVA, F = 68.75, p < 0.001.

Tukey pairwise comparisons

Family error rate = 0.0500
Individual error rate = 0.0104

Critical value = 3.63

TABLE 8.2: Tukey test results for comparison of metamorph emerging from LW at stages 0-4.

Level	0	1	2	3
1	0.002			
2	0.019	0.002		
3	0.012	0.004	0.006	
4	0.025	0.008	0.007	0.013

ANOVA, F = 5.21, p < 0.001.

Tukey pairwise comparisons

Family error rate = 0.0500
Individual error rate = 0.00657

Critical value = 3.86